scientific reports

OPEN

Intact, under-patrolled forests harbor widespread prey but a male-biased tiger population in the Ulu Masen Ecosystem, Sumatra, Indonesia

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Conservation of threatened species is dependent on consistent population monitoring. We present the first status assessment of critically endangered Sumatran tigers (*Panthera tigris sumatrae*) and their prey in the Ulu Masen Ecosystem, Aceh, Indonesia. Our estimates of tiger habitat use are the first reported for a Sumatran ecosystem unprotected at the national level. During 6,732 trap nights accumulated over 23 months of camera-trap monitoring in 2020 and 2022, tigers were detected 39 times at 16 of the 52 stations. We identified 11 individual tigers but sex ratios were highly skewed: 8 males, 1 female, and 2 individuals of unknown sex. Cubs were not photographed either year and we did not observe evidence of tiger reproduction. Tiger habitat use ($\Psi = 0.52$, $SE = 0.15$) was negatively influenced by human disturbance and positively influenced by elevation but those associations were not significant. Our study documents a widespread prey base but uncovers demographic characteristics of tigers indicative of heavy poaching pressures. We conclude that tiger-targeted protection is urgently needed to ensure the species' persistence in Ulu Masen which, together with the adjacent Leuser Ecosystem, represents the largest contiguous tiger conservation landscape remaining in Sumatra.

Keywords Aceh, Camera traps, Habitat use, *Panthera tigris sumatrae*, Sumatra, Sumatran tiger

Large carnivores are integral to Earth's terrestrial ecosystems through their numerous impacts on ecological interactions and processes[1,2]. However, they are also subject to persistent and disproportionately intense pressures from humans[3,4]. Mainly via habitat loss, prey depletion, and poaching, 60% of large carnivores globally have lost more than half of their historic ranges[5]. Many of these species now occur at unnaturally low densities in rugged terrain where they exhibit cryptic behavior, a combination that presents numerous challenges for population monitoring and conservation[6,7]. Ultimately, conservation evaluation and prioritization for large carnivores is dependent on accurate information about their population sizes and trends[8].

In Indonesia, the critically endangered Sumatran tiger (*Panthera tigris sumatrae*) is still present across the Barisan mountain range spanning the western half of the island[9]. The rugged topography has afforded some degree of protection for tigers but it has also complicated collection of essential population data. With very few exceptions, nearly all Sumatran tiger population data originate from protected areas at elevations < 1,000 m above sea level (asl); yet up to 70% of the species' range is found outside protected areas[9]. Consequently, Sumatran tiger conservation is hindered by lack of essential data on the species' population status outside National Parks.

Global tiger conservation strategies are now largely driven by the identification and management of tiger conservation landscapes (TCLs) and source sites. Broadly defined as areas holding tiger source populations that are reproducing above replacement levels and with the potential to maintain > 25 breeding females, source sites are embedded within the larger, previously identified TCLs[10]. Estimated to contain roughly 70% of the world's wild tigers, source sites remain priority areas for tiger research and conservation[11].

Despite original recognition as one of Sumatra's eight source sites in 2010[10], most subsequent range-wide tiger prioritization exercises overlooked Aceh provinces' Ulu Masen Ecosystem (hereafter Ulu Masen),

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instead recognizing the Leuser Ecosystem as northern Sumatra's sole TCL. In fact, of the > 10 range-wide tiger prioritization exercises completed over the past two decades, only four identified Ulu Masen as a TCL[10–13].

Its equivocal status as a TCL aside, Ulu Masen, on the basis of sign-based occupancy surveys and connectivity to the Leuser Ecosystem, remains a global priority for tiger conservation[14]. Despite its extensive lowland and hill forest habitats for tigers, published camera trap-derived data on Sumatran tiger presence in Ulu Masen is limited to a single survey that detected only three tigers in 2017[15]. Consequently, the government natural resource agencies of Aceh have limited tiger population data needed to inform conservation policy and actions in the province.

Our main objective was to provide a comprehensive status assessment of tigers and their main ungulate prey – sambar (*Rusa unicolor*), serow (*Capricornis sumatraensis*), wild boar (*Sus scrofa*), and southern red muntjac (hereafter muntjac) (*Muntiacus muntjac*) – along an elevational gradient in Ulu Masen. Occupancy analyses estimate two important parameters: Ψ, the probability a site is occupied or used by a species; and p, the probability of detecting the species, given its presence[16]. Detection and non-detection data from repeat surveys are used to differentiate these two probabilities[16]. We predicted (a) a strong positive correlation between tiger presence and detection rates of main ungulate prey and (b) greater tiger habitat use at lower elevations. This information is intended to assist government partners with the implementation of a tiger conservation action plan for Ulu Masen.

Results

Data were obtained from 52 of the 61 camera-trap locations (cameras were stolen, malfunctioned, or damaged by elephants (*Elephas maximus sumatrensis*) at 4, 3, and 2 stations, respectively). Our surveys accumulated a total of 6,732 camera-trap nights; cameras operated for 3,477 trap nights in 2020 and 3,255 trap nights in 2022. There was an average of 121 (±88 SD) trap nights per station in 2020 and 141 (±74 SD) trap nights in 2022. Across both years, we recorded 39 photographic detections of tigers at 16 of the 52 stations (naïve occupancy = 0.31). The mean LTD of tigers was 45.2 days (SD 35.8 days, range 7–126 days). At camera stations where a tiger was detected on at least two occasions (n = 9 stations), the mean latency between detections was 32 days (range 1–94 days).

Model-averaged detection probability for tigers was 0.22 (SE = 0.05) (Table 1). Tigers were estimated to occur across 52% (SE = 0.15) of the camera-trap stations, which is 1.7 greater than the naïve estimate of habitat use (Fig. 1). The top-ranked tiger model was negatively influenced by human disturbance and positively influenced by elevation but those associations were not significant (Tables 2 and 3). Male, female, and tigers of unknown sex were detected on 34, 1, and 4 occasions (Fig. 2). From this dataset, we identified 11 tigers: 8 males, 1 female, and 2 individuals of unknown sex. Six of the tigers, including the lone female, were photographed over a 90-day period during the 2020 sampling. With only 3 recaptures of a single, 3-legged male tiger in 2020, there was considerable turnover in individuals. None of the tigers detected in 2020 were detected again in 2022.

Two sympatric predators that have overlapping prey preferences with tigers, the Sunda clouded leopard (*Neofelis diardi*) and dhole (*Cuon alpinus*), were detected 67 and 34 times during our study. At 0.19 (SE = 0.04) and 0.20 (SE = 0.06), detection probabilities for clouded leopard and dhole were slightly lower than those for tiger.

As for prey, we recorded at least one of the four ungulate species at 46 out of 52 camera stations. Sambar, boar, serow, and muntjac were detected at 21, 38, 11, and 48 camera stations, resulting in naïve occupancies of 0.40, 0.73, 0.21, and 0.92, respectively. RAI of ungulate prey averaged 27.86 detections ± 34.55 SD per 100 trap nights at the camera stations. There was considerable variation in detections of prey species among elevation zones (Fig. 3). Sambar habitat use was negatively correlated with elevation (β = -1.33, 0.52 SE) and serow habitat use was positively correlated with distance from forest edge (β = 1.07, 0.49 SE) (Tables 2 and 3). For boar and muntjac, the null site models were the best supported among the competing models, thereby indicating that the covariates did not have significant effects on their habitat use in our study area.

The observed mean LTD of each prey species, given that it was photographed at a camera station, was 26.2 (range = 2-105) days for sambar, 35.1 (2–86) days for serow, 31.6 (1-124) days for boar, and 22.6 (1-186) days for muntjac.

Species	Captures	Naïve	Ψ (SE)	p (SE)	RAI
Sumatran tiger	39	0.31	0.52 (0.15)	0.22 (0.05)	0.58
Dhole	34	0.25	0.43 (0.12)	0.20 (0.06)	0.51
Clouded leopard	68	0.33	0.53 (0.04)	0.19 (0.04)	1.02
Sambar	469	0.40	0.42 (0.09)	0.60 (0.10)	7.01
Wild boar	529	0.73	0.80 (0.08)	0.62 (0.04)	7.87
Muntjac	898	0.92	0.99 (0.03)	0.69 (0.03)	13.31
Serow	75	0.21	0.33 (0.12)	0.24 (0.10)	1.12

Table 1. Camera-trap derived naïve occupancies (Ψ), estimated Ψ, detection probabilities (p), and relative abundance indices (RAI) for tigers, main prey species and other competing Carnivore species in Ulu Masen, Sumatra, Indonesia, 2020 and 2022. Total sampling effort was 6,732 trap nights.

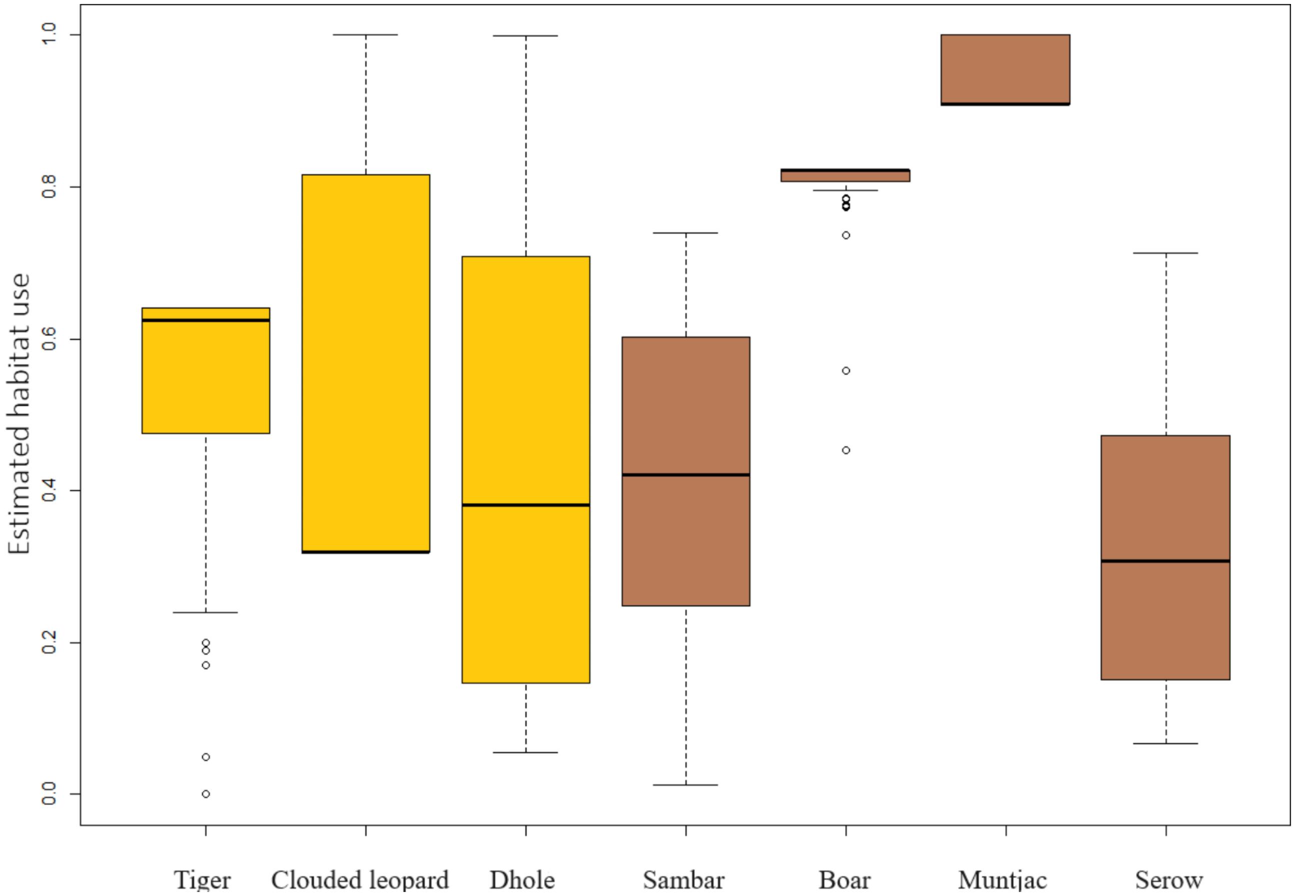

Fig. 1. Boxplots showing estimated habitat use of tigers, sympatric large carnivores, and main ungulate prey species in the Ulu Masen Ecosystem, Aceh, Sumatra, Indonesia, 2020 and 2022.

Discussion

Sumatran tiger conservation requires reliable and representative status assessments[13,17]. Our results provide the first camera trap-derived habitat use estimates of Sumatran tigers and their prey in a nationally unprotected landscape, which comprise up to 70% of the species' range[9]. Due to logistical challenges and funding constraints, most data on Sumatran tiger population status and distribution originate from sign-based occupancy surveys conducted in National Parks[14,18–20]. Despite their utility for informing occupancy models for large carnivores, sign surveys are also prone to observer bias due to inexperience of sampling personnel[21], varying levels of sign detectability (e.g., based on different substrate types across the landscape)[22], and species misidentification by insufficiently trained surveyors (e.g., clouded leopard tracks reported as juvenile tigers, Figel, pers. observ.). Compared to sign surveys, camera-trapping permits more robust estimates of population parameters[23].

Ulu Masen's extensive forest cover and widespread populations of prey, particularly sambar, provide favorable conditions to support tiger conservation and recovery. As the largest prey species in Sumatra, sambar presence is critically important for tigers[24]. An adult sambar killed by a tigress, for example, can provide over 100 kg of edible biomass – sufficient to sustain herself and cubs for up to a week – compared to only ~ 10 kg for the more ubiquitous muntjac.

Compared to our results, sambar are infrequently detected during camera trap surveys of tigers in Sumatra. For example, after 14,013 trap nights, only 15 total sambar detections, among the lowest of all prey species, were recorded in the lowlands of Riau province[25]. In west and north Sumatra only 25 and 16 sambar detections were recorded during 8,984 and 2,857 trap nights, respectively[26,27]. Only in an "Intensive Protection Zone" patrolled by 12 ranger teams in a south Sumatran protected area, did estimates of sambar habitat use ($\Psi = 0.61$, 95% CI 0.40–0.67) exceed ours (0.42, 0.26–0.62)[28].

The relatively widespread sambar occurrence we documented in Ulu Masen is even more significant considering the near-total absence of protected areas in this region. Ulu Masen is designated as a 'Provincially Strategic Area', comprised mostly of protection forest (74%), production forest (12%), and other 'non-forest' areas (14%). Provincially-managed forests receive significantly less funding than National Parks in Indonesia, which are supported by the central government[29]. The 'production' forests mirror the distribution of the region's lowland forests, which are typically preferred habitat of tigers[30].

The identification of 11 tigers during our surveys is suggestive of a sizeable tiger population in Ulu Masen. Only when accounting for site fidelity and sex ratios, do our data tell another story. Despite its crucial importance

Model	AICc	deltaAICc	AIC wgt	Model Likelihood	no.Par.	-2*LogLike
Tiger						
psi(hum), p(elev)	194.33	0.00	0.3506	1.0000	4	185.48
psi(.),p(.)	195.60	1.27	0.1858	0.5299	2	191.36
psi(hum, elev), p(elev)	196.17	1.84	0.1397	0.3985	5	184.87
psi(elev), p(elev)	196.29	1.96	0.1316	0.3753	4	187.44
psi(mp), p(elev)	196.57	2.24	0.1144	0.3263	4	187.72
psi(disted), p(elev)	197.34	3.01	0.0778	0.2220	4	188.49
Sambar						
psi(elev), p(hum)	227.00	0.00	0.3788	1.0000	4	218.13
psi(elev, hum)p(hum)	227.40	0.40	0.3102	0.8187	5	216.07
psi(elev, disted), p(hum)	227.57	0.57	0.2849	0.7520	5	216.24
psi(.),p(hum)	233.69	6.69	0.0134	0.0353	3	227.18
psi(.),p(.)	235.28	8.28	0.0060	0.0159	2	231.03
Serow psi(disted), p(elev)	99.04	0.00	0.3837	1.0000	4	90.17
psi(elev, disted), p(elev)	100.04	1.00	0.2327	0.6065	5	88.71
psi(hum, disted), p(elev)	100.54	1.50	0.1813	0.4724	5	89.21
psi(elev), p(elev)	101.17	2.13	0.1323	0.3447	4	92.30
psi(elev, hum), p(elev)	103.45	4.41	0.0423	0.1103	5	92.12
psi(hum), p(elev)	104.30	5.26	0.0277	0.0721	4	95.43
psi(.),p(.)	123.50	24.46	0.0000	0.0000	2	119.25
Boar						
psi(.),p(disted, hum)	317.92	0.00	0.4740	1.0000	4	309.07
psi(hum), p(disted, hum)	319.54	1.62	0.2108	0.4449	5	308.24
psi(elev), p(disted, hum)	320.05	2.13	0.1634	0.3447	5	308.75
psi(disted), p(disted, hum)	321.68	3.76	0.0723	0.1526	6	307.81
psi(disted, hum), p(disted, hum)	321.90	3.98	0.0648	0.1367	6	308.03
psi(.),p(.)	324.87	6.95	0.0147	0.0310	2	320.63
Muntjac						
psi(.),p(.)	319.85	0.00	0.3798	1.0000	2	315.61
psi(hum), p(.)	319.92	0.07	0.3667	0.9656	3	313.42
psi(disted), p(.)	322.00	2.15	0.1296	0.3413	3	315.50
psi(elev), p(.)	322.09	2.24	0.1239	0.3263	3	315.59

Table 2. Top single-season site-covariate models for Sumatran tigers and prey species in the Ulu Masen Ecosystem, Aceh, Sumatra. We ranked the candidate models in ascending order for each species by their Akaike Information Criterion corrected for small sample size (AICc). Following the "nesting rule", we defined a top model set as all models with Δ AICc ≤ 6 from the best supported model. Abbreviation: disted, distance to forest edge; elev, elevation; hum, human disturbance; mp, main prey.

as a parameter for large carnivore conservation[31], documentation of sex ratio is almost entirely unreported by Sumatran tiger camera-trap studies. After two decades of tiger-targeted camera-trap monitoring in Sumatra, only one study reported the documented composition of males and females: Ten females, four males, and three individuals of unknown sex were identified in Bukit Barisan Selatan National Park[28].

Our results underscore the need to report tiger sex ratios and closely track population dynamics of female tigers, including survival and land tenure patterns. The documentation of females, particularly breeding females, is a key metric for assessing the status of tiger populations and therefore integral to tiger monitoring and recovery efforts[17,28]. Adult female survival is usually the strongest determinant for the growth and persistence of tiger populations[17,32]. Whereas female-biased sex ratios are indicative of healthy tiger populations (considering the species' social organization with the larger home ranges of males overlapping those of several females[33]), high population turnover and male-biased sex ratios generally indicate severe poaching[34,35].

To objectively identify sex of Sumatran tigers, we recommend the placement of two camera traps at each station, with at least one camera programmed to record video. Single cameras operating in photo-only mode without video have a greater likelihood of producing poorly angled pictures that do not permit identification of sex-specific morphology, such as visible genitalia. Only with two cameras at each station can tigers be consistently sexed and identified reliably[8].

Survey duration is another important consideration in camera-trap studies of Sumatran tigers. Resource limitations (e.g., restricted project budgets) and analytical assumptions (e.g., meeting demographic closure) both necessitate shorter sampling timeframes whereas longer camera trap surveys can increase detection probabilities

Species	β (Int) (95% CI)	β (elev) (95% CI)	β (hum) (95% CI)	β (mp) (95% CI)	β (disted) (95% CI)	no Par	AIC	deltaAIC	wi
Tiger	-0.28 (-1.53,0.97)		-2.16 (-5.51,1.19)			4	194.33	0	0.35
	-0.12 (-0.96, 0.72)					2	195.6	1.27	0.19
	-0.35 (-1.55, 0.85)	0.37(-0.59, 1.33)	-1.77 (-4.98, 1.44)			5	196.17	1.84	0.14
	-0.06 (-1.00, 0.88)	0.50 (-0.4, 1.4)				4	196.29	1.96	0.13
	0.06 (-0.98, 1.1)			0.44 (-0.60, 1.48)		4	196.57	2.24	0.11
	0.08 (-0.94, 1.1)				0.25 (-0.63, 1.13)	4	197.34	3.01	0.08
Sambar	-0.47 (-1.16, 0.22)	**-1.25 (-2.23, -0.27)**				4	227	0	0.38
	-0.49 (-1.22, 0.24)	**-1.33 (-2.35, -0.31)**	-0.65 (-1.87, 0.57)			5	227.4	0.4	0.31
	-0.46 (-1.17, 0.25)	-1.39 (-2.41, -0.37)			0.54 (-0.26, 1.34)	5	227.57	0.57	0.28
	-0.32 (-0.91, 0.27)					3	233.69	6.69	0.01
	-0.30 (-0.89, 0.29)					2	235.87	8.28	0
Serow	-0.88 (-2.06, 0.3)				**1.07 (0.11, 2.03)**	4	99.04	0	0.38
	-1.21 (-2.27, -0.15)	0.58 (-0.36, 1.52)			0.88 (-0.1, 1.86)	5	100.04	1	0.23
	-1.19 (-2.52, 0.14)		-1.15 (-3.82, 1.52)		**1.15 (0.13, 2.17)**	5	100.54	1.5	0.18
	-1.08 (-2.06, -0.1)	0.83 (-0.03, 1.69)				4	101.17	2.13	0.13
	-1.11 (-2.11, -0.11)	0.80 (-0.08, 1.68)	-0.27 (-1.64, 1.10)			5	103.45	4.41	0.04
	-0.56 (-1.76, 0.64)		-0.56 (-2.32, 1.2)			4	104.3	5.26	0.03
	-1.22 (-1.91, -0.53)					2	123.5	24.46	0
Boar	1.38 (0.60, 2.16)					4	317.92	0	0.47
	1.41 (0.61, 2.21)		-0.30 (-0.91, 0.31)			5	319.54	1.62	0.21
	1.39 (0.59, 2.19)	-0.21 (-0.94, 0.52)				5	320.05	2.13	0.16
	1.43 (0.61, 2.25)	-0.26 (-1.00, 0.48)	-0.33 (-0.94, 0.28)			6	321.68	3.76	0.07
	1.41 (0.61, 2.21)		-0.29 (-0.90, 0.32)		0.20 (-0.64, 1.04)	6	321.9	3.98	0.06
	1.49 (0.65, 2.33)					2	324.87	6.95	0.01
Muntjac	4.35 (-1.6, 10.31)					2	319.85	0	0.6
	4.72 (-1.75, 11.19)				-1.00 (-6.35, 4.35)	3	322	2.15	0.2
	4.37 (-1.55, 10.29)	0.21 (-3.36, 3.78)				3	322.09	2.24	0.2

Table 3. Parameter estimates and 95% credible intervals (CI) from top models influencing habitat use of tigers and their prey in the Ulu Masen Ecosystem. Covariates are considered to have a significant influence on habitat use when their 95% CI did not overlap zero (marked in bold). Abbreviation: int, intercept; elev, elevation; disted, distance to forest edge; hum, human disturbance; mp, main prey.

and improve precision of estimates[6]. Despite these tradeoffs, our results indicate that erroneous inferences could arise from occupancy analyses of data collected from short-term surveys. To account for the LTD and average time intervals between photographs, we recommend placement of cameras for at least six months when surveying for Sumatran tigers, which occur at low densities in even the best protected lowland forests[30,36]. This is double the length of most previous studies, which usually maintain cameras for 2–3 months[25,28,37]. Such "snapshot" surveys are likely to produce underestimates of true occupancy due to the elevated risk of recording false absences. False absences, one of the major sources of bias in occupancy surveys, can inflate true absences if surveys are not conducted for sufficient timeframes[16].

Based on our results, we identify an urgent need for boosted tiger-targeted protection in Ulu Masen. Snares present the greatest immediate threat to Sumatran tigers and their prey in this landscape[38,39] and in many areas of Sumatra[4,40] and southeast Asia[41]. In Ulu Masen the only tiger we photo-recaptured had 3-legs, most likely the result of limb loss from snare entrapment[38]. Between 2008–2023, we identified 6 tiger snaring incidents occurring either inside or within 100 km of our study area[4]. It is important to consider this number as a minimum estimate because we have no way to estimate the unknown number of tigers that either died or escaped from snares.

Rangers have demonstrated impacts on reducing threats of these traps. In the first rigorous assessment of the effectiveness of rangers for protecting Sumatran tigers, ranger networks resulted in a 41% reduction of snares set in Kerinci-Seblat National Park[42]. Similar gains in Ulu Masen are unachievable without a boosted ranger network. One of the key challenges to the implementation of tiger conservation programs in this landscape is the ability to efficiently monitor expansive roadless areas with very limited personnel. Considering the size of Ulu Masen, we estimate the need for an additional 560–640 trained rangers, numbers consistent with documented tiger recoveries in Thailand[43].

In the past two decades, Sumatran tiger protection in Ulu Masen was most notably supported by a multi-year, landscape-scale monitoring program initiated in 2011 when the government of Aceh partnered with Fauna and Flora International to implement an innovative community ranger program. For three years, rangers from 28 forest-edge communities conducted patrols to remove snares, monitor endangered wildlife, and report wildlife crime. The program was a working example of effective community-based forest protection until funding ended in 2014[44]. From 2014–present, only our surveys and a 6-month camera-trap survey in 2017 provided any form

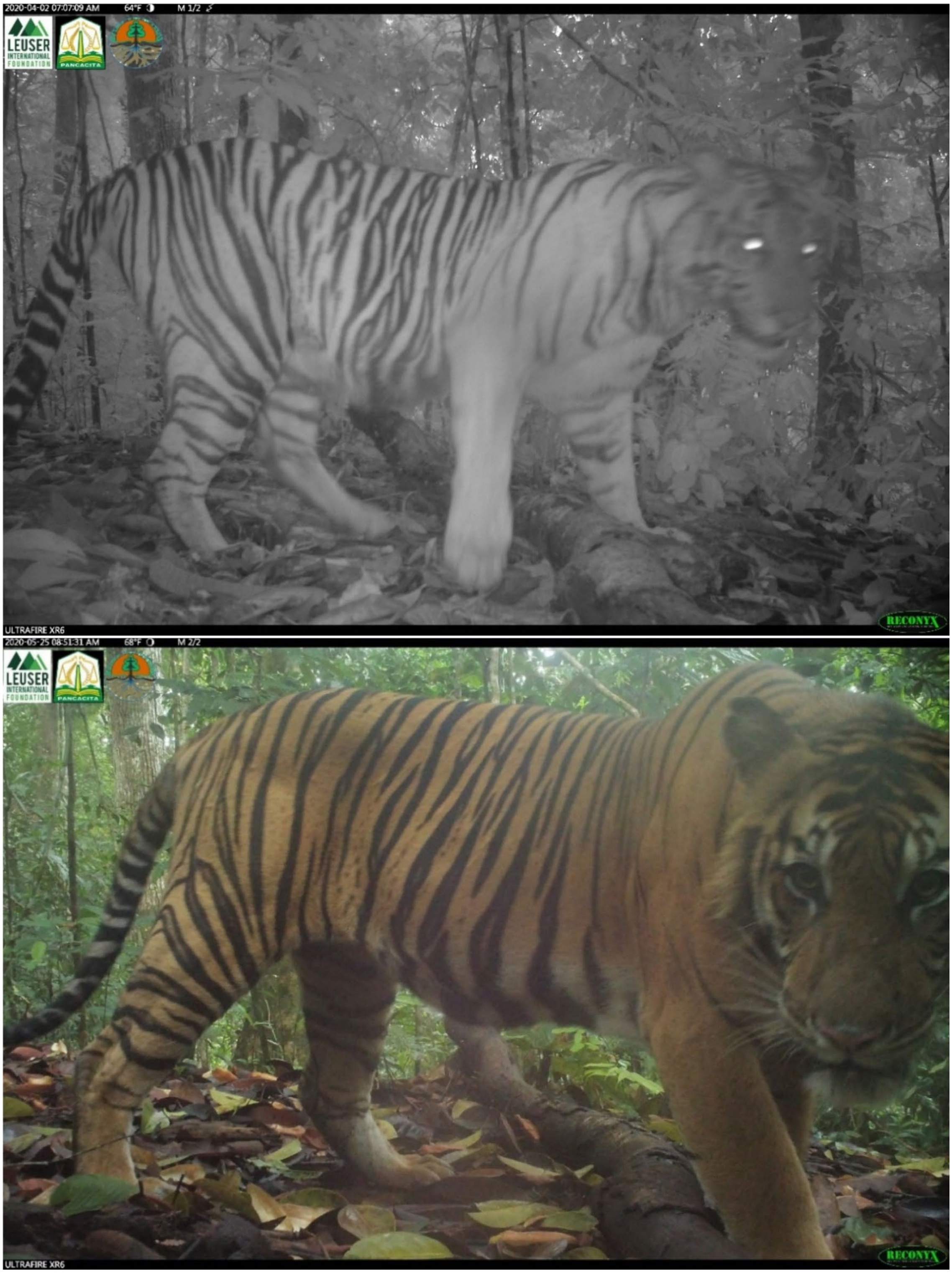

Fig. 2. The lone female and one of eight male Sumatran tigers (*Panthera tigris sumatrae*) detected in the Ulu Masen Ecosystem, Aceh, Indonesia. These individuals were photographed in submontane forests at the same station, 53 days apart, in 2020.

of tiger-targeted patrols[15]. Spatiotemporal gaps in conservation programs are regularly associated with declines of tigers, which are dependent on consistent, year-round protection[45].

Unfortunately, tiger range–especially in Southeast Asia–has not been surveyed uniformly nor patrolled consistently. As a result, some reported gains in tiger populations are likely more of a reflection of factors such

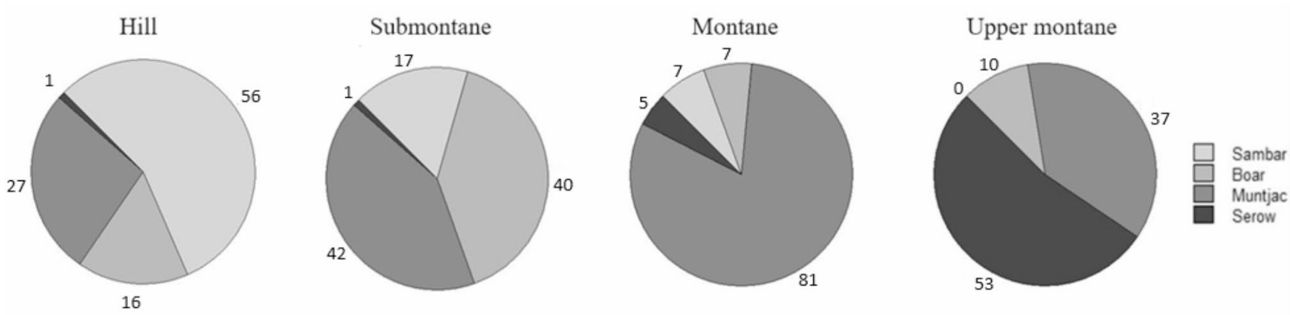

Fig. 3. Prey compositions along an elevational gradient in the Ulu Masen Ecosystem, Aceh, Sumatra, Indonesia, 2020 and 2022.

as improved sampling protocols and advancements in camera-trap technology than any real increase in tiger numbers[7,46].

Another limitation common among tiger camera-trapping studies is the inability to sample the same sites over numerous years. Our surveys, which were interrupted by the emergence and spread of COVID-19, prevented sampling during 2021, when the expansion of our originally planned camera polygon was halted. Multi-year surveys permit better estimates of the distribution, survival, and site fidelity exhibited by individual tigers[17].

Nonetheless, our survey results permit valuable insights into the status of tigers in Ulu Masen where their habitat use, for example, exceeds camera trap-generated estimates from other locations in Sumatra, including National Parks in Riau, where average tiger occupancy was 0.43 [25]. Our estimates are lower, however, than tiger occupancies ($\Psi = 0.65$) recorded in a protected area of southern Sumatra[28]. More long-term monitoring, driven by scientifically rigorous protocols, will permit greater comparison and insights into priority areas for Sumatran tiger conservation.

Methodology
Study site
The Ulu Masen Ecosystem in Aceh province is a 9,500 km² forest block adjacent to the 26,500 km² Leuser Ecosystem, which covers both Aceh and part of the neighboring province of North Sumatra. Topography in Ulu Masen ranges from lowland rainforest at 200 m asl to the peak of Gunung Peuët Sagoë at 2785 m asl. Approximately 50% of Ulu Masen occurs at elevations below 800 m asl. Average annual precipitation is c. 2,500 mm/year. Besides extensive stands of mixed Dipterocarp forests are pockets of Sumatran tropical pine forests, represented, primarily, by the range-restricted Merkus's pine (*Pinus merkusii*)[47].

Ulu Masen is managed at the provincial level under the jurisdiction of forest management unitsoverseen by *Dinas Lingkungan Hidup dan Kehutanan* (DLHK; Environment and Forestry Service of Aceh). Its wildlife is managed at the national level by *Balai Konservasi Sumber Daya Alam* (BKSDA; Natural Resources Conservation Center). Besides the 80 km² Jantho Nature Reserve, protected areas are entirely lacking from Ulu Masen[48] and unpermitted logging is widespread in the ecosystem[49].

Our camera polygon spanned 462 km² and covered parts of three districts in Aceh province: Aceh Tengah, Pidie, and Bireuën. Based on Indonesian government data, the population of these districts is approximately 1.09 million people (115 people/km²)[50]. Approximately 10% of this human population is based in two major towns – Bireuën, and Takengon – both located within 30 km of our camera polygon.

Our camera polygon was 98.3% forested. There is one village – with approximately 1,530 residents – located along the southern border of our polygon. Among a small network of dirt roads, there is small-scale water buffalo (*Bubalus bubalis*) ranching in the southeastern portion of our study area.

Sampling design
In accordance with other tiger surveys in northern Sumatra[15,26,36], we overlaid 4 × 4 km grid cells over our study area and placed two, un-baited camera-traps at the stations, with at least one camera station inside each grid cell. We followed the grid protocol to facilitate better comparison with other survey sites.

Identifying tiger habitat use requires distinguishing between availability of, and preference for, habitats[51]. Thus, we used a stratified random sampling design for camera deployment, stratifying our gridded study area into four elevation zones. We selected the number of sites proportional to the amount of land area within each elevation zone.

Within each zone we secured paired cameras including one photo camera (Reconyx® HC500 or HC600) and one video camera (Reconyx® HF2X or XR6). We powered the photo cameras with Tenergy® NiMH rechargeable batteries and video cameras were powered with Energizer® lithium batteries. Cameras were attached ~ 40–45 cm above ground-level to trees along forest ridges, which are known travel pathways of both tigers and their main ungulate prey: Sambar, serow, wild boar, and muntjac[52]. The paired set-up, with cameras positioned 3–4 m from both sides of the trail, permitted simultaneous detections of passing tigers, thereby allowing us to (a) distinguish individuals based on distinctive stripe patterns and (b) identify their sex based on the presence of visible genitalia[53]. Cameras were programmed to record a 2- or 3-image burst and, for the HF2X and XR6 models, a 10-second video when triggered.

Sampling areas included four elevation zones: Hill (300–800 m asl), submontane (801–1400), montane (1401–2000), and upper montane (2001 +) forests. Each zone supports unique soil compositions and floral assemblages which influence the presence of prey species and, in turn, tigers[30,54].

To assess habitat use of tigers and their main ungulate prey in Ulu Masen, we conducted two camera-trap surveys. During the first survey, which ran from February–December 2020, we deployed cameras at 33 stations at an average elevation of 1330 m asl (± 550 SD). During the second survey, conducted between January–December 2022, we deployed cameras at 28 stations at an average elevation of 1053 m asl (± 292 SD). Cameras placed in 2022 were in distinct locations, not sampled in 2020. To increase our ability to assess habitat use patterns of tigers and their prey, we combined the data across both years. Occupancy analyses of large carnivores occurring at naturally low densities–such as rainforest tigers–requires extended sampling to obtain sufficient data[6]. Since longer sampling periods violate the demographic closure assumption of single-season models, we interpret the occupancy parameter, Ψ, as 'probability of habitat use'[16].

Across both surveys, cameras were placed at elevations ranging from 630–2621 m asl. Average camera spacing was 2.2 km (± 0.86 SD). We used photographic 'captures" from camera-traps, sorted into 30-day sampling occasions. These detection data from each station were subsequently inserted into detection matrices for tigers and their ungulate prey: Sambar, serow, wild boar, and muntjac. Species-specific detection histories consisted of 23 sampling occasions, each 1 month in duration, where the tiger or ungulate prey species was either detected (1) or not detected (0) at a given camera trap station.

We calculated a relative abundance index (RAI: # of independent detections of tigers and their prey/100 trap nights). We do not interpret RAI as an index of abundance but rather as the likelihood for a tiger to encounter an ungulate at the camera trap stations[55]. In the case of large-bodied and more easily detectable herbivores, RAI estimates can provide reliable indices of prey availability for large carnivores[56].

We also reported a key, but often overlooked, metric in tiger camera-trap studies: Latency to initial detection (LTD). We defined LTD as the number of days until the first photograph of a tiger or a main prey species at a site. This metric serves as an indicator of the effort required to detect tigers and their prey; these sampling timeframes can vary substantially across tiger-occupied landscapes[7,53].

To estimate the probability of use at each camera station, we fit single-season, single-species occupancy models using PRESENCE v. 2.13.47[57]. Occupancy models correct for variance in species detectability by using presence/absence (detection/non-detection) data to estimate the proportion of sites occupied by the target species[16]. These surveys assess the environmental variables (covariates) associated with species' occurrence patterns. Prior to analysis, we transformed continuous covariates into standardized z-scores (x – x/σ).

We used a multi-step approach to model selection by first estimating univariate effects of each covariate only on probability of detection. We included four covariates: Elevation, distance from forest edge, RAI of main ungulate prey, and, as a metric of human disturbance, RAI of humans detected on cameras. The next step was including only the most supported detection covariates in models assessing the effects of covariates on site occupancy[16]. We tested covariates for collinearity using Pearson's correlation test and used an $r > 0.6$ threshold to exclude covariates from the same model[58].

We ranked the candidate models for each species by their Akaike Information Criterion corrected for small sample size (AICc). Following the "nesting rule"[59], we defined a top model set as all models with Δ AICc ≤ 6 from the best supported model.

Data availability

The datasets generated and/or analysed during the current study are not publicly available due to the critically endangered status of the study species and its high susceptibility to poaching but are available from the corresponding author on reasonable request.

Received: 16 June 2024; Accepted: 7 October 2024
Published online: 24 October 2024

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Acknowledgements
We are grateful to Bapak A. Hanan and Bapak Muhammad Daud of Aceh's Department of Environment and Forestry. Suhada Arief assisted GIS analyses and LIF ranger Kamal Khairi provided key support during 2022 surveys. Dewi Wahyuni was instrumental for organizing ranger expeditions. The Fulbright program, administered by the American Indonesian Exchange Foundation (AMINEF), provided helpful support with logistical procedures in Jakarta. Research permits, facilitated by AMINEF, Universitas Syiah Kuala, and the Leuser International Foundation, were issued by BKSDA-Aceh, DLHK, and the Indonesian Ministry of Research, Technology, and Higher Education (RISTEKDIKTI) (permit number: 365/E5/E5.4/SIP/2019).

Author contributions
Conceptualization, J.J.F; formal analysis, J.J.F.; investigation, J.J.F.; writing – original draft preparation, J.J.F., writing – review and editing, J.J.F., R.S., S.F.B., M.H.; supervision, R.S., S.F.B., and M.H.; project administration, J.J.F. and R.S.; funding acquisition, J.J.F.

Declarations

Competing interests
The authors declare no competing interests.

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