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Research Article

Camera trap distance sampling for density estimation of tiger prey in a Sumatran ecosystem restoration concession

Beno Fariza Syahri[1,*], **Febri Anggriawan Widodo**[1,2,*], **Muhammad Rahmad Al Kahfi**[3], **Muhammad Rizki Qosyim**[3], **Heri Irawan**[1], **Dede Hendra Setiawan**[1], **Muhammad Ali Imron**[1,4], **Matthew J. Struebig**[2], **Nicolas J. Deere**[2], **Satyawan Pudyatmoko**[4,5] **and Thomas Neill Edward Gray**[6]

[1]World Wide Fund for Nature (WWF) Indonesia, Jakarta, Indonesia
[2]Durrell Institute of Conservation and Ecology, University of Kent, Canterbury, UK
[3]Perseroan Terbatas Alam Bukit Tigapuluh, Jambi, Indonesia
[4]Wildlife Laboratory, Faculty of Forestry, Universitas Gadjah Mada, Yogyakarta, Indonesia
[5]Directorate General of Nature Resources and Ecosystem Conservation, The Ministry of Forestry of the Republic of Indonesia, Jakarta, Indonesia
[6]World Wide Fund for Nature (WWF) Tigers Alive Initiative, Kuala Lumpur, Malaysia

Correspondence: Beno Fariza Syahri (bsyahri@wwf.id) and Febri Anggriawan Widodo (faw7@kent.ac.uk)

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Estimating prey species densities is critical for implementing effective tiger *Panthera tigris* recovery strategies. Several statistical models exist for density estimation of unmarked species from camera trap data, all of which rely on the random placement of cameras. This has limited the use of such models, as random camera trap placement is often viewed by field conservationists as impractical and inefficient, particularly in landscapes where ungulates are rare. We used camera trap distance sampling (CTDS) to estimate the density of prey species from randomly placed cameras within an ecosystem restoration concession in central Sumatra. We estimated densities of two species: southern red muntjac *Muntiacus muntjak* (2.14 ± SE 0.8 individuals per-km^2) and southern pig-tailed macaque *Macaca nemestrina* (6.43 ± SE 1.2 individuals per-km^2). These represent the first quantitative density estimates for these species from tiger landscapes within the Sundaic forests of South-east Asia. Uncertainty around the density estimates was likely due to the low sample size of camera trap locations, which led to high variability in the number of encounters between camera traps. Whilst detections of other tiger prey species (i.e. sambar *Rusa unicolor*, wild pig *Sus scrofa*, bearded pig *S. barbatus*) were insufficient to estimate density, trap success rates of these species were higher than camera traps set in a conventional tiger-focused grid. Complementary camera trap survey designs that implement both targeted and randomized placement designs are likely to provide a better picture of carnivore populations and critical resources, whilst minimizing bias, in Asian tropical forests. Tiger prey density within the site is low, presumably due to a combination of gun-hunting of ungulates by local communities, and disease, particularly African swine fever affecting pig species. Recovering tigers across the extensive rainforests of Sumatra will require targeted ungulate hunting reduction and active prey recovery, particularly focusing on sambar and wild pigs.

Keywords: camera trap, density estimation, hunting, management, restoration concession, unmarked

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*Shared last authorship.

Introduction

Recovering tiger *Panthera tigris* populations depend on accurate estimates of the densities and trends of their primary prey, which directly influence tiger persistence and recovery strategies (Harihar et al. 2018). Across Asia, many ungulate tiger prey species face severe hunting pressure and rapid habitat loss, yet their ecology in tropical rainforests remains poorly documented (Gray 2018, Phumanee et al. 2020, McShea et al. 2025). The recent emergence of African swine fever further highlights the urgency of robust monitoring frameworks that are capable of detecting sudden population declines (Luskin et al. 2020, Lieb et al. 2025).

Estimating densities of unmarked ungulates in Asian rainforests is particularly challenging. Low animal densities, dense vegetation, and rugged terrain reduce detectability and render traditional line transect surveys impractical (Karanth and Nichols 2017, Gray 2018, Phumanee et al. 2020). Camera trap distance sampling (CTDS) has emerged as a promising alternative, using detection distances from camera traps to estimate animal density (Howe et al. 2017, Cappelle et al. 2021). Yet, its application in tropical Asia has been limited due to stringent assumptions, concerns about efficiency when species are rare, and the logistical difficulties of implementing truly random camera placement (Waller et al. 2024, Camp et al. 2025).

Camera trap placement itself is a central issue. Wildlife surveys using camera traps can be conducted through targeted placement, where cameras are positioned along features such as roads, trails, or water sources; or through random placement, where cameras are distributed independently of such features. Targeted sampling, particularly along trails, has become the standard in tiger landscapes as it maximizes detections of large carnivores and enables individual identification for capture–mark–recapture or spatially explicit capture–recapture (SECR) analyses (Karanth and Nichols 2017, Ash et al. 2020). However, methods such as CTDS require random placement to satisfy model assumptions (Howe et al. 2017, Palencia et al. 2021). This has raised concerns among field biologists, who question whether randomly placed cameras in dense tropical forests will yield sufficient detections, especially of rare species, and whether the additional effort is justified. Moreover, camera trapping needs to consider bias in species detections; for example, some species tend to have higher detection probability in targeted trail-based deployments, which are known to favor certain taxa such as large carnivore species, whilst some other species may avoid trails or favor other features, thus making other camera trap deployment strategies more appropriate (Camp et al. 2025, Greco et al. 2025). Dealing with these concerns, it is important to directly implement quasi-experimental surveys (i.e. standardized procedures for targeted species and random placement strategies at the same location during overlapping sampling periods) to understand how the placement strategy may influence detectability.

Sumatra provides a critical setting in which to address these questions. The island encompasses approximately 54 000 km^2 of tiger conservation landscapes (TCLs) (Goodrich et al. 2022, Sanderson et al. 2023), yet the population status and trends of both tigers and their prey remain uncertain across much of the region (Wibisono and Pusparini 2010, Luskin et al. 2017). Given escalating threats to Sumatran tigers, there is an urgent need to develop conservation programs that address tigers, their prey, and habitat connectivity (Figel et al. 2024).

Ecosystem restoration concessions (ERCs) are Indonesia's initiative to legally license non-state actors to manage designated limited production forest areas in the country, targeting to bend the curve of deforestation by restoring degraded areas, alongside safeguarding biodiversity and benefiting local communities (Brancalion et al. 2019, Harrison et al. 2020, Sayer et al. 2021). As the Sumatran tiger occurrence primarily relies on large contiguous forest blocks with linkages to other habitats, such as mosaics of plantations and smaller forest patches (Sunarto et al. 2012), ERCs are expected to serve as tiger habitats beyond primary protected areas and can have other critical functions, including connectivity.

In this study, we applied CTDS to estimate the density of tiger prey species within an ERC located in the buffer zone of a protected area, Bukit Tigapuluh National Park, in central Sumatra. To our knowledge, this study represents the first density estimates for tiger prey in Sundaic tropical forests, which support approximately 10% of the global tiger population and over 70% of South-east Asia's tigers (Goodrich et al. 2022). Additionally, to evaluate the implications of camera placement, we compared species detections between randomly placed cameras (for CTDS) and cameras deployed using a targeted, tiger-focused approach. Whilst there were some spatial and temporal differences between the two (random and targeted) camera trap deployments, this comparison provides insight into how placement strategy influences species detections and informs the feasibility of applying CTDS to monitor tiger prey species in tropical forests of Asia.

Material and methods

Study site

The study was conducted within Block I (221 km^2) of the Perseroan Terbatas Alam Bukit Tigapuluh (henceforth PT. ABT), an ERC, in Tebo Regency, Jambi Province, Sumatra (1°10′48”S, 102°31′50”E, Fig. 1). The concession forms part of the buffer zone of Bukit Tigapuluh National Park: a protected area covering 1431 km^2, which in 2012 had an estimated tiger population of between 12 and 32 individuals (Luskin et al. 2017). The current tiger population within the protected area is unknown, but between three and five individuals, including one resident breeding female, have been camera-trapped within PT.ABT since 2020 (Widodo et al. unpubl.). Putative tiger prey species within PT.ABT are sambar *Rusa unicolor*, wild pig *Sus scrofa*, bearded pig *S. barbaratus*, southern red muntjac *Muntiacus muntjak*, and southern pig-tailed macaque *Macaca nemestrina,* whilst sympatric carnivores include dhole *Cuon alpinus* and Sunda clouded

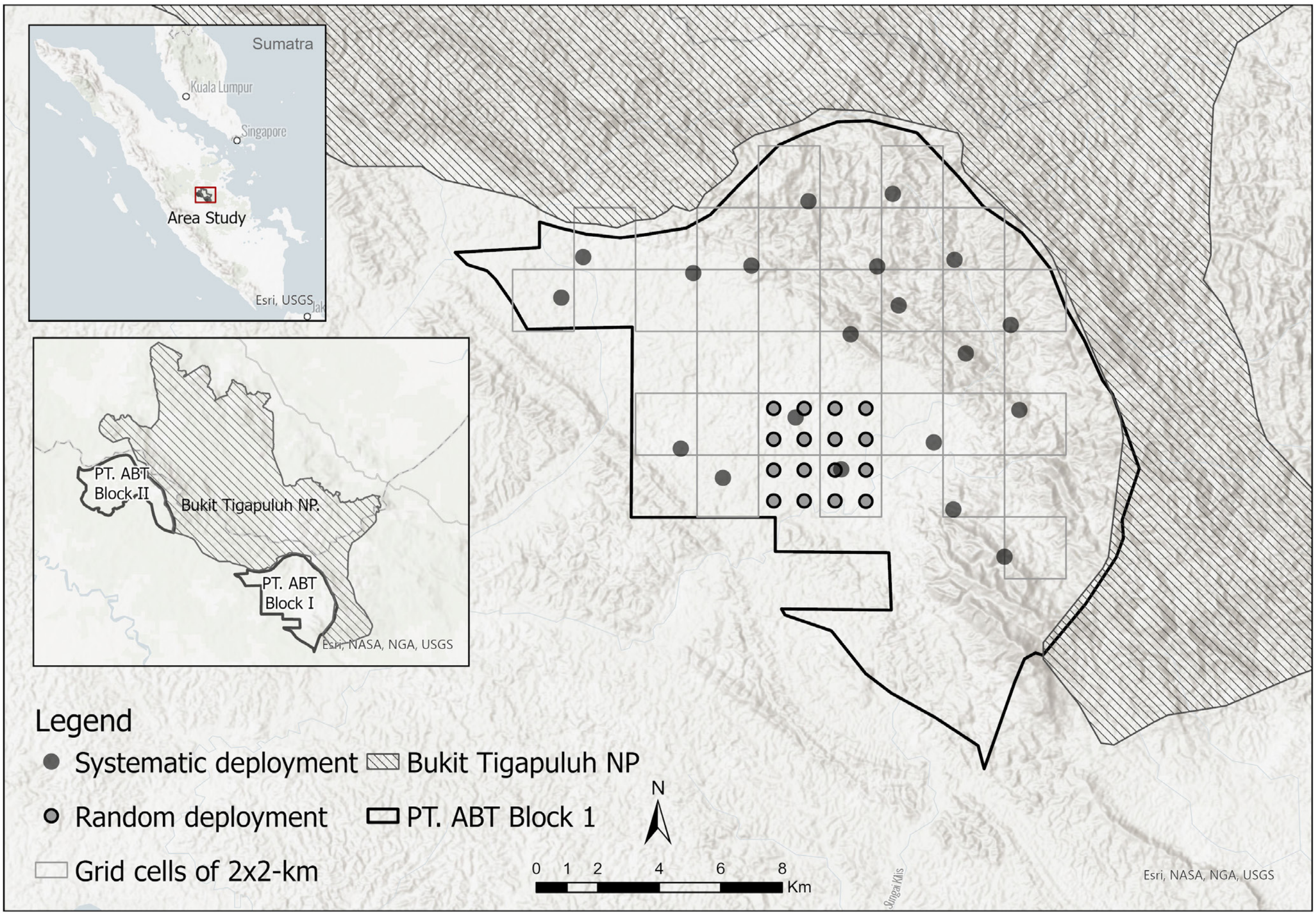

Figure 1. Map of Block I of Perseroan Terbatas Alam Bukit Tigapuluh (PT. ABT) ecosystem restoration concession in the Bukit Tigapuluh conservation landscape, central Sumatra, with locations of random and targeted placement of camera traps.

leopard *Neofelis diardi*. PT.ABT is a tropical rainforest area with an average rainfall of 2577 mm per year, temperature between 20.8° and 33°C, and altitude between 60 and 843 m a. s. l. (Rahman et al. 2023). The landscape is also home to Sumatran native indigenous communities: Talang Mamak and Orang Rimba, who are highly dependent on forest resources (Prasetijo 2021).

Camera trap study design

We deployed camera traps under two different techniques: random placement and targeted placement between December 2023 and June 2024 (Fig. 1; Supporting information). The random and targeted camera -traps were both operational between January and March 2024, with the random cameras placed earlier (December 2023) and the targeted cameras removed later (June 2024). For the random placement, a 4 × 4-km grid (16-km^2) was assigned to guide camera trap deployment and a total of 16 Reconyx PC800® cameras was placed on the nearest tree to the exact co-ordinates of the center of each grid cell. This was generally between 3 and 5 m of the exact center of the grid cell, depending on GPS accuracy. All cameras were set at maximum sensitivity with no quiet period and set to take one picture per trigger event. Cameras were deployed facing north (0°), approximately 30–50 cm above the ground, with the sensor angled parallel to the ground surface. Where necessary, vegetation immediately in front of the cameras was carefully cleared. This design represents a random deployment of cameras meeting the assumptions of sampling and animal movement inherent within distance sampling (Howe et al. 2017). CTDS requires random camera trap placement because it assumes cameras sample space independently of animal movement features, producing an unbiased distribution of detection distances and encounter rates across habitats. Targeted placement along trails or roads violates this assumption and can systematically bias density estimates (Howe et al. 2017).

For targeted deployment, 22 camera trap stations were established along trails and other habitat features designed to maximise encounters with tigers. At each station, a pair of Reconyx PC800/PC850® and Bushnell NatureView/Trophycam® cameras were placed opposite each other to photograph both flanks of tigers for individual identification. Camera stations were spaced between 1 and 4 km apart (Supporting information), with the minimum convex hull of the camera trap array being 114 km^2. This study design is widely applied for monitoring tigers (Ash et al.

2020) and other cryptic mammal species (Linkie et al. 2013, Sibarani et al. 2024), through by-catch across Asia. The area sampled by the targeted cameras was larger than the area sampled by the randomly placed cameras, with corresponding differences in the topography, if not the underlying forest type, between the survey areas. Approximately half of the targeted cameras were set in flat lowland forest, directly comparable to the area surveyed by the random cameras.

Data management

All photographs were extracted, catalogued, and managed in standardized spreadsheets. We identified and renamed all mammal photographs (of identifiable species > 1 kg) based on the object recorded, date and time modified, camera and memory card ID, and placement station ID.

To quantify the influence of placement strategy on species representation, we estimated trap success rate (TSR, the number of pseudo-independent detections per 100 trap nights) and trap prevalence (the proportion of camera trap stations from which a species was detected) (Widodo et al. 2022) for both the random and targeted survey designs. As is de rigueur in camera trap studies in Asia, we used a 30-min interval to define pseudo-independence (O'Brien et al. 2003), whilst recognizing that independence is inferred as opposed to robustly documented (Peral et al. 2022). Hence, we prefer and promote the use of the term pseudo-independence. To account for potential differences in detectability between the two placement strategies, we also compared multispecies camera trap level probabilities of occupancy and detection, and p-values for species with > 3 detections by using a simple Bayesian multispecies occupancy framework (Deere et al. 2020, Devarajan et al. 2020). We did not include habitat covariates in our models.

Camera trap distance sampling (CTDS)

We used CTDS to estimate the density of tiger prey species from camera trap detections under a random placement strategy (Rowcliffe et al. 2011, Howe et al. 2017, Palencia et al. 2021, Haucke et al. 2022). CTDS adapts conventional distance sampling to camera traps by combining information on detection distances, animal activity, and survey effort to derive density estimates. In simple terms, the method assumes that animals moving through the camera's field of view are sampled in a series of 'snapshots', and the probability of detection declines with distance from the camera.

For each animal detection, we estimated the distance from the camera to the animal using a photogrammetry approach (Haucke et al. 2022). Each camera was calibrated in the field by photographing a calibration board at 1-m intervals from the camera center, allowing us to relate pixel size to true distance. Distances were then extracted from animal images using this calibration (Fig. 2). When multiple individuals appeared in a frame, we recorded the distance to each animal separately.

Within CTDS, sampling effort is a product of the angle of view of the camera (Θ) and the number of predetermined

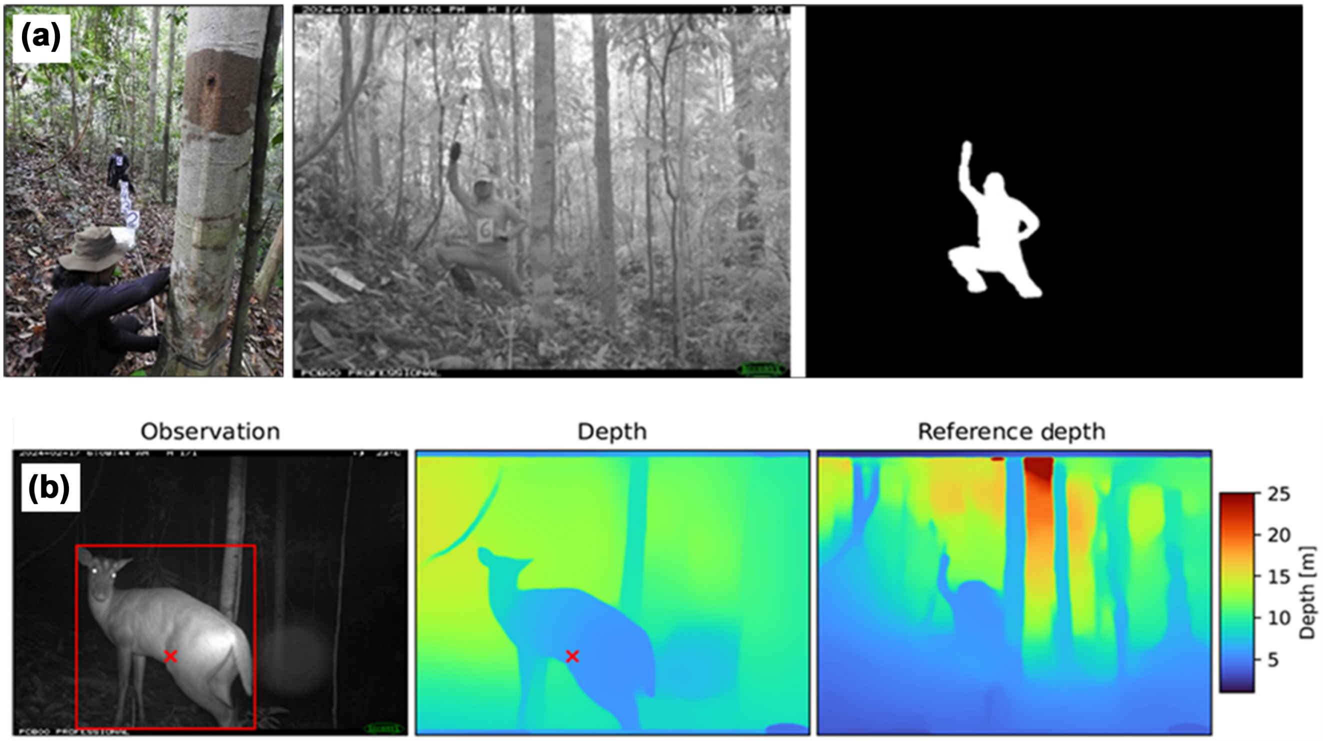

Figure 2. (a) Camera trap distance sampling (CDTS) measurement and calibration process of the distance. (b) An example of a camera trap image of southern red muntjac *Muntiacus muntjak*, with depth and reference depth for measuring the distance of the observed species in front of the installed camera.

snapshot moments, which represent the opportunities for a camera to obtain an image of an animal (Miles et al. 2024). CTDS density estimates are strongly influenced by the values for the snapshot interval, which account for the 're-set' time between photographs when a camera trap is not operating (Kühl et al. 2023). We estimated the effective snapshot interval empirically from image sequences. Across all independent detection events, we identified 1-min periods during which the target animal was clearly present within the camera viewshed for the full duration of the minute. The number of photographs recorded during each period was counted, and the mean number of images per minute was calculated across events. The snapshot interval was similar for all species (Supporting information) with a mean of ~ 20 photographs minute^{-1} when an animal was continuously present, corresponding to an effective snapshot interval of approximately 3 s. This empirically derived snapshot interval was used in subsequent distance sampling analyses. Based on camera trap manufacturer specifications and our field tests, we used 60° as the angle of view. Sensitivity analysis on our data suggested that density estimates changed by between 7.5 to 10% per 5° difference in the angle of view (Supporting information), highlighting the need to consider angle of view in analysis.

Population density (D) is then estimated as:

$$D = \frac{y}{\pi W^2 \mathrm{epa}}$$

where y is the number of detections of each species, w is the truncation distance (beyond which detections were disregarded to avoid right-skewed detection functions), p is the average detection probability within the effective detection zone, a is the activity level (i.e. the proportion of time the species is active), and e overall sampling effort which is a product of spatial and temporal effort (as described above).

Detection probability was estimated by fitting detection functions to the observed distribution of detection distances for each species. Candidate models included half-normal, hazard-rate, and uniform key functions with cosine or Hermite polynomial adjustments (Thomas et al. 2010). Model selection was based on The Quasi-Akaike Information Criterion (QAIC), where the lowest value corresponds to the best-performing detection function. Detection functions were fitted separately for each focal species.

Because camera traps only detect moving animals, CTDS requires an estimate of the proportion of time each species is active (Palencia et al. 2024). We estimated activity patterns independently for each species by fitting circular kernel density functions to time-of-day data using the R package 'activity' (Rowcliffe et al. 2014). To avoid inflation from long detection sequences, we used pseudo-independent events (separated by ≥ 30 min). The resulting activity level and standard error were incorporated as multipliers in the density estimation. For group-living animals, such as wild pigs and primates, detection probability could be influenced by group size, with potentially larger groups of animals being able to be detected at larger distances. We evaluated group size effects on detection distance and found no evidence of a relationship (Supporting information) and group size was therefore not included as a covariate in the detection function.

Results

Comparison of detection rates between random and targeted cameras

The randomly placed cameras operated for a total of 1833 trap nights, capturing 16 species of mammals (Supporting information). The targeted cameras operated for a similar sampling effort (1838 trap-nights) and detected 23 species of mammals (Supporting information). One key tiger prey species, sambar, was only detected from the randomly placed cameras, whilst eight species of small to medium carnivore, including globally threatened and ecologically significant species such as Sunda clouded leopards and dholes, were only detected from the targeted cameras (Fig. 3, Supporting information). TSRs for ungulate tiger prey species and primates were generally higher from randomly placed cameras, whilst carnivores, including tigers, were more frequently detected from targeted cameras which were deliberately targeted on trails and other features believed to be preferred by tigers (Fig. 3; Supporting information). Bayesian estimates of camera trap level occupancy and detection probability were also generally similar between the two camera trap deployments, with credible intervals of all species overlapping (Supporting information).

Camera trap distance sampling (CTDS) for prey density estimates

Distance and encounter data were extracted for four possible tiger prey species: southern red muntjac, sambar, wild pig, and southern pig-tailed macaque (Supporting information). Whilst > 50 measured distances were obtained for each species, the small number of pseudo-independent detections for wild pigs (16) and sambar (6) resulted in a clumped distance distribution inappropriate for further analysis using a CTDS framework (Supporting information).

The estimated activity level for southern red muntjac and southern pig-tailed macaque was similar (Table 1; Supporting information). The best fitting distance-sampling models were hazard rate with no adjustment, and hazard rate with one adjustment, for southern red muntjac and southern pig-tailed macaque, respectively (Fig. 4). Density of southern red muntjac was estimated at 2.14 ± SE 0.76 individuals per km^2. Density of southern pig-tailed macaque was estimated at 6.43 ± SE 2.00 individuals per km^2 (Table 1). The CVs of both estimates were relatively wide (Table 1) – likely a result of the variation in encounter rate between cameras. For southern red muntjac, ~ 57% of the encounters came from 3 of the 16 camera stations, whilst for southern pig-tailed macaque, 72% came from just four stations. A longer sampling duration and possibly more cameras would likely reduce such variability in inter-camera detection rates.

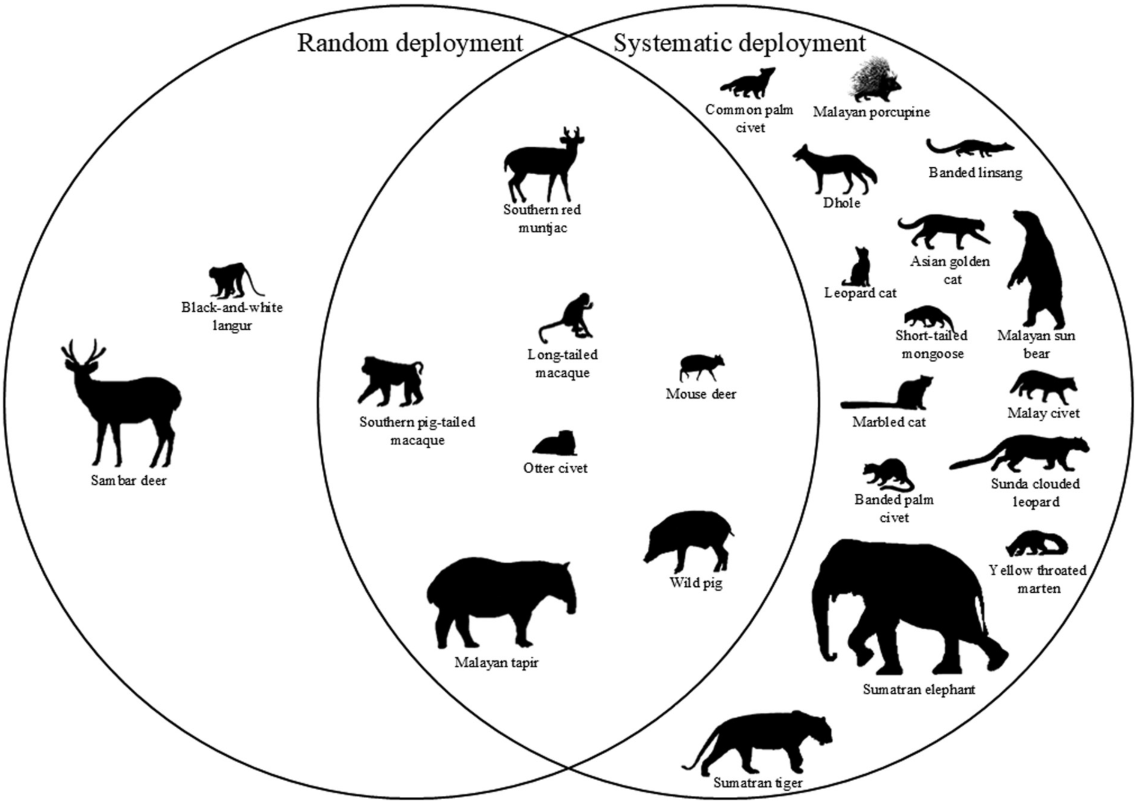

Figure 3. Comparison of species-specific detection rate (based on trap success rate) between randomly deployed and targeted camera-traps within Perseroan Terbatas Alam Bukit Tigapuluh (PT. ABT) Block I. Species with > 20% difference in trap success rate (TSR) between deployment types are shown in separate sectors of the Venn diagram.

Discussion

We demonstrate the utility of CTDS for monitoring ungulate and primate prey species in Sundaic rainforests, marking its first application in Indonesia. The country is a globally significant biodiversity hotspot, but it faces severe anthropogenic pressures (Benítez-López et al. 2019, Struebig et al. 2025). We provide some of the first published density estimates for tiger prey in South-east Asian tropical forests, though the precision of our estimates was relatively low. Expanding the number of sampling sites and extending the study duration would improve the robustness of future estimates, particularly for scarcer species. A major constraint in unmarked species density estimation is the requirement for random camera placement (Palencia et al. 2021), which field biologists in Asia often perceive as logistically impractical (authors, unpubl.). However, our results indicate that random placement did not hinder detections of ungulates and primates under the conditions of this study, with detection rates similar or higher than those from targeted, tiger-focused camera traps.

Nevertheless, carnivores such as tigers and Sunda clouded leopards were less frequently detected on random grids, highlighting the value of combining random and systematic placement to balance ecological monitoring and conservation objectives (Wearn et al. 2013, Gray 2018, Greco et al. 2025).

Table 1. Camera trap distance sampling parameters for the best selected models for southern red muntjac *Muntiacus muntjak* and southern pig-tailed macaque *Macaca nemestrina* (hazard rate with no adjustment, and hazard rate with one adjustment, respectively).

Parameter	Parameter description	Muntjac	Pig-tailed macaque
n	Number of detections	391	2198
K	Number of sampling points	16	16
w	Truncation distance (m)	15	15
ˆt	Snapshot (s)	3	3
ϴ	Angle (rad)	1.05	1.05
P	Probability of detection (± SE)	0.09 ± 0.01	0.12 ± 0.004
A	Availability of detection (± SE)	0.30 ± 0.07	0.37 ± 0.03
EDD	Effective detection distance (m)	4.5	4.06
D	Population density (ind/ km^2) (± SE)	2.14 ± 0.8	6.43 ± 1.20
CV	Coefficient of variation	0.35	0.31

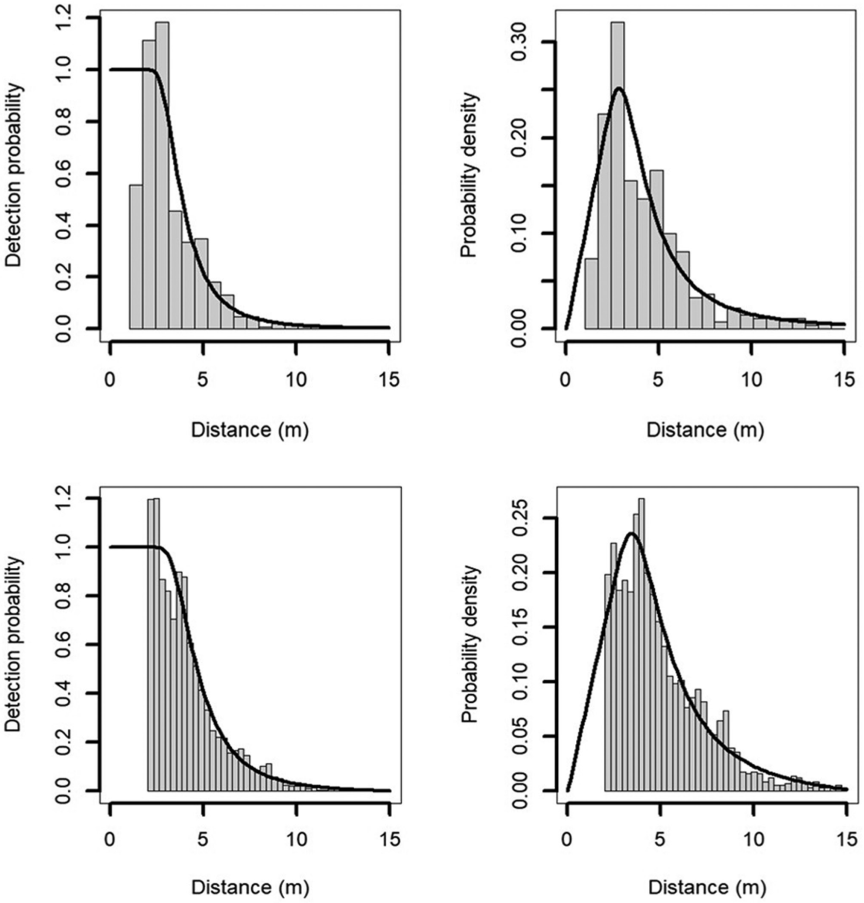

Figure 4. Detection probability graph (left) and probability density graph (right) as a function of distance for the best model selected for southern red muntjac *Muntiacus muntjak* (top) and southern pig-tailed macaque *Macaca nemestrina* (bottom).

Due to unavoidable logistical and financial constraints, the spatial and temporal sampling differed between the random and targeted sampling grids, and this variation could impact the mammal communities within the grids. This caveat should be considered when comparing the camera trap detection rates between the random and targeted camera traps. For almost all species, occupancy and detection probabilities – as well as p-values from simple Bayesian models – were largely similar between the two camera trap deployments, further highlighting the value of inferences from randomly placed cameras for understanding mammal communities.

Our estimate of southern red muntjac density (2.1 individuals / km^2, ± SE 0.8) is lower than that reported by Wearn et al. (2022) based on a random encounter model from camera-trapping in lowland forests in Sabah, Malaysia (> 4.0 individuals / km^2). Our density also falls toward the lower end of values reported for the ecologically similar northern red muntjac *Muntiacus vaginalis* across Asian tiger landscapes, which range from < 0.5 to nearly 10 individuals / km^2 (Groenenberg et al. 2023, Adhikari et al. 2024, Aziz et al. 2025). Although low, our estimate is ecologically plausible for an evergreen tropical forest where prey densities are typically depressed compared to more productive habitats. Importantly, this represents the first published density estimate for southern red muntjac from a Tiger Conservation Landscape. The role of *Muntjac* spp. in tiger diets remains uncertain. Across most published studies from South and mainland South-east Asia, muntjac contribute relatively little compared to larger prey such as sambar, chital *Axis axis*, or wild pig (Andheria et al. 2007, Hayward et al. 2012, Steinmetz et al. 2021). However, tiger diet in Sumatra is poorly documented and it is unclear whether muntjac play a more significant role in this island context where larger prey species are naturally less abundant.

In our study site, larger ungulates appear to be particularly scarce, reflecting broader patterns of herbivore declines across the globe (Ripple et al. 2015). Wild pigs were detected infrequently, likely reflecting the impact of African swine fever, which has caused widespread declines across Sumatra since 2020 (Luskin et al. 2020, Lieb et al. 2025). Bearded pigs, once present, have not been recorded since the African swine fever outbreak. Sambar, already the rarest large deer on Sumatra, were also detected at very low rates, consistent with other studies in central Sumatra (Widodo et al. 2022). Together, these findings suggest that the prey base for tigers is currently limited, with muntjac potentially playing a proportionally greater role than in mainland systems. Despite these constraints, PT. ABT continues to support a small but resident tiger population, with three and five individuals detected annually since 2020, including evidence of breeding females (Widodo et al. unpubl.). The persistence of tigers and other carnivores indicates that the landscape retains its conservation value, but sustaining these populations will require active prey recovery actions.

Unfortunately, hunting remains a major threat to the area, as our camera traps detected suspected hunters at night carrying homemade guns to presumably shoot ungulates. We believe these hunters are largely local indigenous community members who are hunting for a combination of personal consumption, local trading within their villages, and for sale to outsiders and subsequent transportation to urban consumers. Ungulate species such as wild and bearded pigs, sambar, and muntjacs are preferred targets for indigenous community hunters, with wild pig meat primarily demanded and consumed in Jambi Province, especially by non-Muslims (Luskin et al. 2013). Unlike other parts of Sumatra, snaring and hunting with dogs appear to be limited here (Gray et al. 2018, Figel et al. 2021, Kartika et al. 2025), but direct shooting pressure is clearly suppressing prey populations and placing hunters in direct competition with tigers. Effective anti-poaching strategies are therefore essential. These should combine strengthened patrols and deterrence with community-based interventions that provide alternative livelihoods and protein sources, alongside targeted behavior-change programs for known hunters (Linkie et al. 2015, Risdianto et al. 2016, Kartika et al. 2025). Ultimately, reducing hunting pressure and restoring ungulate populations are prerequisites for securing long-term tiger survival and population recovery in this landscape.

Conclusion

We demonstrate that CTDS is applicable within Sundaic rainforests and show that random placement of camera traps did not reduce detection rates of tiger prey. We also highlight that a larger sample size of camera trap stations would be necessary to improve the precision of our density estimates and recommend more studies to implement CTDS to estimate tiger prey densities in South-east Asia. We found low densities of key prey species in a Sumatran restoration concession, likely due to hunting and disease impacts. We suggest that recovering tigers across the extensive rainforests of Sumatra likely requires integrating targeted ungulate hunting reduction and may need active prey recovery, particularly focusing on sambar and wild pigs.

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Conflict of interest – The authors declare no conflict of interest.

Author contributions

Beno Fariza Syahri: Conceptualization (equal); Data curation (equal); Formal analysis (equal); Methodology (equal); Visualization (equal); Writing – original draft (equal); Writing – review and editing (equal). **Febri Anggriawan Widodo**: Conceptualization (equal); Formal analysis (equal); Funding acquisition (equal); Methodology (equal); Visualization (equal); Writing – original draft (equal); Writing – review and editing (equal). **Muhammad Rahmad Al Kahfi**: Data curation (equal). **Muhammad Rizki Qosyim**: Data curation (equal). **Heri Irawan**: Visualization (equal). **Dede Hendra Setiawan**: Writing – review and editing (equal). **Muhammad Ali Imron**: Writing – review and editing (equal). **Matthew J. Struebig**: Writing – review and editing (equal). **Nicolas J. Deere**: Writing – review and editing (equal). **Satyawan Pudyatmoko**: Writing – review and editing (equal). **Thomas Neill Edward Gray**: Conceptualization (equal); Formal analysis (equal); Methodology (equal); Writing – original draft (equal); Writing – review and editing (equal).

Data availability statement

Data are available from the Dryad Digital Repository: https://drive.google.com/drive/folders/1tLN1SEM3N9nYAIoEfOfSLJT-HXACWo8p?usp=sharing (Syahri et al. 2026).

Supporting information

The Supporting information associated with this article is available with the online version.

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