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Rigorous assessment of a unique tiger recovery in Southeast Asia based on photographic capture-recapture modeling of population dynamics

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ABSTRACT

Tigers and other large predatory carnivores have suffered population extirpations and range contractions. This is particularly true for tiger populations in southeastern Asia, which harbours one-third of their remaining habitats. In stark contrast, a sustained recovery of a wild tiger population has occurred between 2007 and 2023, in three reserves of Thailand: Huai Kha Khaeng (HKK), Thung Yai East (TYE) and Thung Yai West (TYW), which together cover 6470 km^2 (36 %) of the larger Western Forest Complex (WEFCOM). We quantitatively monitored this recovery employing closed and open model analyses of data from photographic capture-recapture sampling. The resulting estimates of tiger population dynamic parameters showed: mean (±SE) tiger abundance annually varied from 36 (1.0) to 79 (1.53) in HKK, 2 (0.26) to 20 (4.45) in TYE and 3 (0.26) to 44 (2.11) in TYW, driven by mean annual survival rates of 0.79 (0.02) in HKK, 0.72 (0.05) in TYE, and 0.69 (0.05) in TYW. The annual numbers of recruits fluctuated from 0 (1.69) to 33 (1.93) tigers in HKK, 0 (0.47) to 13 (0.57) in TYE and 0 (1.13) to 36 (2.28) in TYW. Overall, the mean tiger population densities/100 km^2 ranged between 1.3 (0.19) and 2.9 (0.29) in HKK, 0.2 (0.08) and 1.8 (0.34) in TYE, and 0.2 (0.07) and 3.1 (0.56) in TYW. Generally, the tiger population trended upward, with reserves protected over longer periods leading the tiger recovery. Our results are further backed by ancillary records on births of 67 cubs, 47 tiger dispersal events, as well as the recovery corresponding with incremental spatio-temporal coverage by the patrols. Cumulatively, our results provide evidence that effective law enforcement should be a critical component for achieving tiger population recoveries in Asia. Alternative conservation strategies that ignore this component do not appear to be evidence-based. Our results also demonstrate the utility of the independent collaborative monitoring framework adopted by the Thailand Government.

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1. Introduction

1.1. The historical context of tiger conservation

Population recovery of apex predators in tropical Asia poses serious challenges arising from direct poaching, over-hunting of prey species as well as large-scale loss and degradation of habitats (Chapron et al., 2008; Karanth et al., 2004; Nuwer, 2018). These pressures on large predators such as the tiger, are rooted in rising numbers and economic aspirations of human populations (e.g., (Trisurat and Havmoller, 2018; Krishnasamy and Zavagli, 2020), (Rostro-García et al., 2023). Tigers have suffered a massive range contraction of ~92 % in historical times (Sanderson et al., 2023). In southeastern Asia, coarse-scale reviews (Goodrich et al., 2022) confirm recent extirpation of wild tigers from entire countries of Cambodia, Lao PDR, and Viet Nam as well as from most of Myanmar, Peninsular Malaysia, and Indonesia. In southern Asia, a few tiger population recoveries have been documented in the past five decades (Karanth et al., 2020; Jhala et al., 2021). In contrast, in southeastern Asia despite supporting ~33 % of remaining potential tiger habitats range-wide (Sanderson et al., 2023), such recoveries have been scarce, and evidence presented in support have mostly lacked rigorously estimated demographic parameters based on long-term population dynamic studies employing well-established methods (Karanth and Nichols, 2017).

Robust studies of population dynamics are integral to adaptive management of threatened animal populations using structured decision-making approaches (Williams et al., 2002). The key population dynamic parameters, however, are difficult to estimate in wild tigers because of their elusiveness, low ecological densities, territorial as well as wide-ranging behaviors. These problems are compounded by extensive spatiotemporal scales necessary in studies of wide-ranging carnivores such as tigers (Karanth and Nichols, 2017).

In this context, tiger population recovery observed in the Western Forest Complex (WEFCOM) of Thailand over two decades presents a stark contrast. Early attempts to assess the status of wild tigers in Thailand relied on ad hoc sample surveys of expert opinion (Rabinowitz, 1993; Smith et al., 1999), which yielded country-wide estimates of population size of 250–500 tigers. Subsequently, a report by the Wildlife Conservation Office of Government of Thailand (2010) employing a combination of ad hoc camera-trapping and field surveys of tiger spoor, yielded an estimate of 180–252 tigers, with the WEFCOM region putatively harboring ~60 % (107−148) of them.

The first quantitative population assessment in Thailand (Simcharoen et al., 2007) applying photographic capture-recapture (CR) methods (Karanth and Nichols, 1998) yielded a density of 3.98 tigers/100 km^2 (SE 0.51) over an area of 477 km^2 (SE 58.24) in Huai Kha Khaeng (HKK) Wildlife Sanctuary within WEFCOM. Contrasting these estimates with much higher densities measured at ecologically similar sites in India (Karanth et al., 2004), Simcharoen et al., (2007) speculated that the WEFCOM region could potentially support as many as ~2,000 wild tigers under effective protection, highlighting the importance of the region for global tiger recovery.

Subsequently, the Government of Thailand intensified its tiger protection efforts in WEFCOM in the mid-2000s. Uniquely, it also initiated a rigorous tiger population monitoring system (Duangchantrasiri et al., 2016), based on robust photographic capture-recapture methods (Royle et al., 2017). This monitoring generated reliable estimates of demographic parameters such as tiger population density, abundance, rates of change as well as of key drivers like survival and recruitment. A separate radio-telemetry study of tigers yielded sex-specific estimates of tiger home range sizes and movement rates (Simcharoen et al., 2014), which assisted in the delineation of state-space (Royle et al., 2014) required for spatial capture-recapture modelling.

Results of the initial camera trap study in HKK (Duangchantrasiri et al., 2016) showed that within an area of 2,780 km^2 (trap array ranging between 624 and 1,026 km^2), mean tiger densities varied between 1.3 and 2.1 tigers/100 km^2 with annual apparent survival rates of 80–96 %, and numbers of recruits varying between 0 and 24 tigers during 2005–2012 when anti-poaching patrolling and protection efforts gradually intensified. The tiger densities attained in HKK over this 8-year period were higher compared to those observed elsewhere in southeastern Asia but were much lower than densities of 5–15 tigers/100 km^2 attained in comparable habitats in India and Nepal following intensified protection over 20–30 years.

Encouraged by these results, the Thailand Government and collaborators expanded the surveys to cover adjacent protected areas of Thung Yai East (TYE) and Thung Yai West (TYW), which had shorter histories of protection as well more intensive adverse human impacts than HKK (WEFCOM, 2004). Here, we report the data, analyses and insights gained from our present study of tiger population dynamics during the 2007–2023 period across the expanded area of 5,300 km^2.

1.2. Scope and objectives

Empirical observations over the past fifty years indicate that direct protection interventions are among the key factors that have led to observed tiger recoveries in a few protected reserves across Asia (Walston et al., 2010). These include: depression of hunting pressures on prey and tigers through effective anti-poaching patrols and other law-enforcement measures; reduction/elimination of biomass extractive pressures such as forest product removal and livestock grazing; and, reduction of human population densities in critical tiger habitats through incentive-driven voluntary resettlement schemes to prevent intrusion of developmental projects, reduce habitat fragmentation and improve connectivity among tiger populations. While a host of other interventions, such as human-tiger conflict mitigation, measures that enhance human socio-economic welfare and conservation education can also potentially augment tiger recovery efforts, we hypothesize that without the key protection measures being put in place, demographic recoveries of tigers are unlikely to occur particularly in the absence of any rigorous evidence that supports the alternative model of tiger recovery.

Within this overall context, we aim to confront two primary *a priori* hypotheses in this study: (1) tiger populations in HKK, TYE and TYW are likely to show an increase in densities over time or at least show a population growth rate of >1 in response to stronger and sustained protection efforts implemented since 2006; and (2) expected apparent survival rate is likely to be higher in HKK than in TYE and TYW based on history and current levels of protection in the three study sites.

Using long-term population monitoring data and rigorous analyses, we test these hypotheses through two specific objectives:

1. To model and estimate tiger demographic parameters including population density and abundance; survival and recruitment using spatially explicit closed CR models as well as open CR models under a robust design, and
2. Examine these parameters in the context of history and effectiveness of law enforcement efforts observed in the study area and elsewhere.

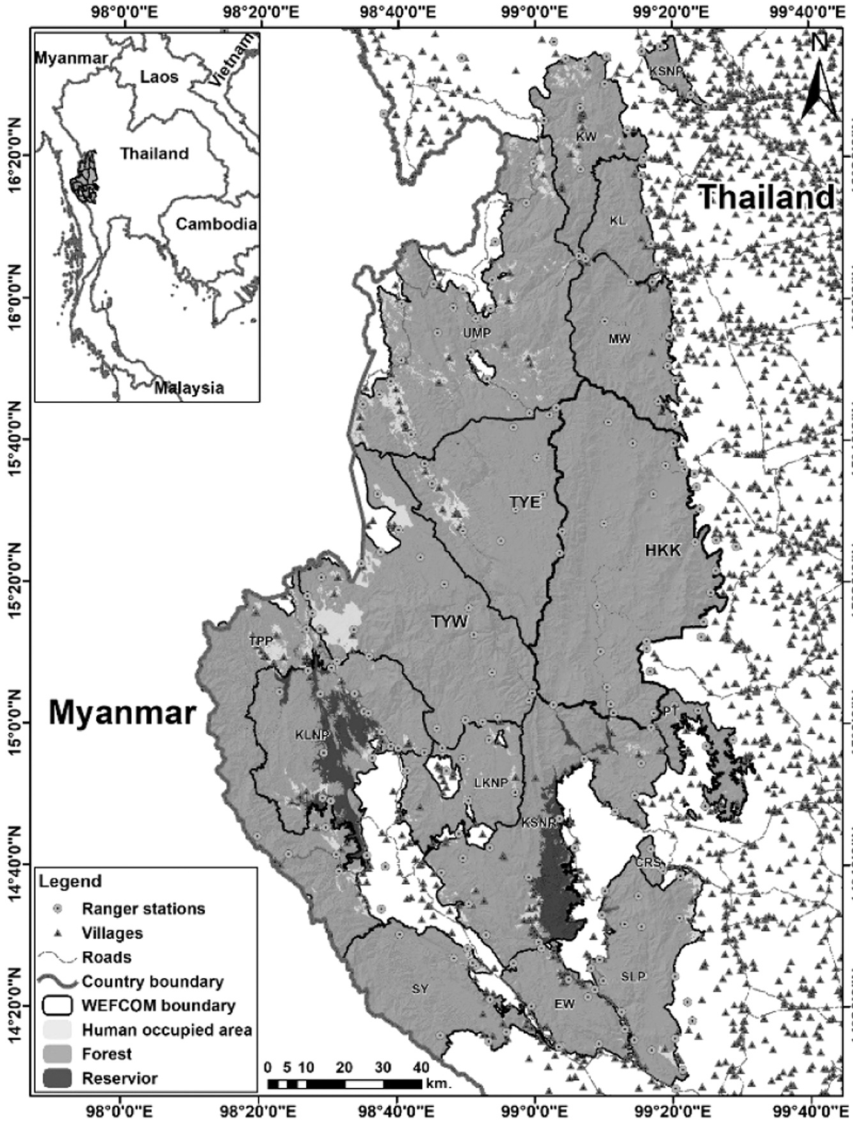

Fig. 1. Map showing the Western Forest Complex (WEFCOM), forest areas, ranger stations, villages, and human settlements. Huai Kha Khaeng (HKK), Thung Yai East (TYE), and Thung Yai West (TYW) Wildlife Sanctuaries constitute a UNESCO World Heritage Site and together form Thailand's core tiger Source Site. Fourteen other Protected areas included in WEFCOM are Umpang (UMP) Wildlife Sanctuary (WS), Klong Wang Chao (KW) National Park (NP), Klong Lan NP (KL), Mae Wong NP (MW), Khao Sanam Preang NP (KSP), Salakpra WS (SLP), Sai Yok NP (SY), Erawan NP (ERW), Khuean Srinagarindra NP (KSN), Phu Toei NP (PT), Chalerm Rattanakosin NP (CRS), Lum Klong Ngu NP (LKN), Khao Laem NP (KLNP), and Tong Pha Phum NP (TPP). The whole forested landscape of WEFCOM is ~18,000 km^2. The inset map shows the location of WEFCOM within Thailand.

2. Materials and methods

2.1. Study area

WEFCOM, one of the largest designated tiger-recovery landscapes in Southeast Asia, consists of a network of 17 contiguous protected areas (Fig. 1) covering over ~18,000 km^2. Our study was conducted in three large, adjoining wildlife sanctuaries, Huai Kha Khaeng (HKK; area: 2780 km^2), Thung Yai Naresuan East (TYE; area: 1572 km^2) and Thung Yai Naresuan West (TYW; area: 2118 km^2), which form the core of this landscape (WEFCOM, 2004). The study area, hereafter HKK-TY (coordinates: 14°56′-15°48 N Lat., 98°25′-99°28′E Long; altitude: 200 – 1800 m; annual precipitation: 1500 – 2400 mm), is also designated as a UNESCO World Heritage Site to protect overall biodiversity as well as ecological and evolutionary processes (UNESCO World Heritage Committee, 1991). These three sanctuaries differ in their vegetation types, proportions of area under human impacts as well as in their histories of poaching and law enforcement efforts countering such threats, which are fully described in WEFCOM (WEFCOM, 2004). The overall habitat diversity in WEFCOM together with various management interventions (WEFCOM, 2004; Simcharoen et al., 2014; Duangchantrasiri et al., 2016; Voravann, 2017) have resulted in productive tiger habitats comparable to those in India where tiger-prey assemblages have attained high densities consequent to long term protection (Karanth et al., 2004). Particularly, prey populations are recovering in HKK-TY (Saisamorn et al., 2024) in direct contrast to their declining trend observed elsewhere in southeast Asia (Corlett, 2007; Ripple et al., 2015; Gardner et al., 2016; Groenenberg et al., 2020).

Significantly, a systematic patrolling system improving on monitoring protocols such as MIKE (IUCN, 1998) and MIST (Stokes,

Table 1
Details of camera trap surveys of tigers in Huai Kha Khaeng (2004/2005–2023), Thung Yai East (2008–2023) and Thung Yai West (2007–2023) in WEFCOM, Thailand.

Site	Season	No. of days of sampling	Sampling mid-point	Δt (years)	No. of camera trap locations	Trap-array area (km^2)	Effort (trap-days)	No. of tigers photo-captured	Cumulative no. of tigers photo-captured
HKK	2004–2005	481	06-Oct-2004	1.41	155	524	910	24	24
	2006	185	04-Mar-2006	1.04	137	624	2,156	27	36
	2007	135	20-Mar-2007	1.01	156	991	2,597	26	41
	2008	145	23-Mar-2008	0.92	180	982	2,999	34	50
	2009	149	20-Feb-2009	1.08	175	991	2,714	31	59
	2010	143	22-Mar-2010	0.98	181	934	3,003	29	68
	2011	133	15-Mar-2011	1.01	183	905	3,013	33	81
	2012	145	19-Mar-2012	1.00	174	991	3,342	34	87
	2013	138	18-Mar-2013	0.98	181	991	3,365	36	97
	2014	124	10-Mar-2014	1.00	171	991	2,972	35	107
	2015	120	09-Mar-2015	1.00	175	991	2,948	38	115
	2016	121	08-Mar-2016	0.98	174	991	2,868	31	119
	2017	106	02-Mar-2017	0.84	166	991	5,220	46	139
	2018	106	01-Jan-2018	1.00	170	991	5,528	41	148
	2019	104	31-Dec-2018	0.99	175	991	5,574	45	162
	2020	110	28-Dec-2019	1.01	174	991	5,769	43	173
	2021	110	31-Dec-2020	1.00	169	991	5,975	47	185
	2022	112	30-Dec-2021	0.99	178	991	5,724	53	197
	2023	108	27-Dec-2022	-	174	991	5,793	58	211
TYE	2008	37	29-Nov-2007	3.01	41	295	674	5	5
	2011	39	2-Dec-2010	2.01	45	215	691	4	9
	2013	43	3-Dec-2012	1.98	37	295	1,061	6	14
	2015	46	28-Nov-2014	2.03	33	295	1,200	3	15
	2017	41	6-Dec-2016	1.33	37	295	1,165	5	18
	2018	60	6-Apr-2018	0.99	33	295	1,407	13	26
	2019	58	2-Apr-2019	1.01	35	295	1,496	10	27
	2020	56	3-Apr-2020	1.01	39	295	1,295	9	28
	2021	58	5-Apr-2021	1.01	36	295	1,269	9	29
	2022	59	7-Apr-2022	0.98	34	295	1,440	16	37
	2023	55	1-Apr-2023	-	35	295	1,342	20	47
TYW	2007	36	05-Dec-2006	2.98	36	176	666	7	7
	2010	36	25-Nov-2009	2.02	42	166	671	4	9
	2012	37	02-Dec-2011	2.01	45	170	713	3	12
	2014	45	04-Dec-2013	1.99	30	176	1,119	6	16
	2016	43	01-Dec-2015	1.06	30	176	1,121	9	21
	2017	66	24-Dec-2016	1.28	35	176	1,105	4	22
	2018	53	03-Apr-2018	1.00	30	176	1,261	4	23
	2019	59	03-Apr-2019	1.00	31	176	1,503	9	28
	2020	50	01-Apr-2020	0.99	31	176	1,046	6	28
	2021	45	29-Mar-2021	1.02	31	176	964	9	32
	2022	57	07-Apr-2022	0.98	32	176	1,412	6	32
	2023	50	29-Mar-2023	-	35	176	1,214	16	43

2010) was introduced in HKK in 2006 to curb poaching and other anthropogenic pressures (DNP, 2022b). This monitoring system, subsequently renamed as SMART (Spatial Monitoring And Reporting Tool), also included intensive training and capacity building of protection personnel (DNP, 2022b). The SMART system was extended in 2009 to cover TYE and TYW, and by 2014 the rest of the PAs within WEFCOM were covered. Both the patrolling frequency and spatial coverage gradually increased over time (WCS Thailand, 2013); see also Table 6). Currently, HKK-TY is protected by 52 patrol stations, with ~500 active-duty wildlife rangers covering >70 % of the study area with an average annual patrol frequency of 20 visits/km^2 (DNP, 2022b). This law-enforcement capacity (~8 rangers/100 km^2; WCS Thailand, 2019) is nearly 5–8 times higher than other comparable protection system existing elsewhere in southeast Asia (<1 ranger/100 km^2 in Kerenci-Seblat NP in Western Sumatra; Linkie et al., 2003, ~1 ranger/100 km^2 in Srepok WS in Cambodia and ~1.5 rangers/100 km^2 in Taman Negara NP in Malaysia; SMART patrol report, 2019).

2.2. Field surveys

Camera trap data were generated using field protocols developed in India (Karanth and Nichols, 2002) and implemented in HKK (Duangchantrasiri et al., 2016). Each camera trap location had two cameras positioned to capture stripe patterns on opposite flanks of passing tigers enabling unambiguous identification of individuals. Trap locations were placed along forest trails to maximize capture probabilities based on signs of past usage by tigers. Camera traps were placed 3–4 km apart, based on spatial design considerations (Karanth and Nichols, 2002; Karanth and Nichols, 2017) that included expected tiger home range sizes derived from radio-telemetry studies in HKK (Simcharoen et al., 2014; Simcharoen et al., 2022).

In HKK, the camera trap arrays were of 524–991 km^2 size, with 137–183 trap locations, in each of the 19 annual primary sampling periods between 2005 and 2023 (see Table 1, Fig. 2). Based on terrain conditions and availability of equipment, the trap array was split into 2–8 blocks during each survey. The camera traps were stationed at each location for 15–30 successive days, and then moved around. Because the sampled areas in 2004–05 and 2006 were smaller and their primary sampling periods (see Table 1) far exceeded the closure period (Karanth and Nichols, 2002; Karanth and Nichols, 2017), we excluded abundance estimates from these two years for estimating numbers of recruits and population change. The remaining primary sampling periods (2007–2023) ranged between 104 and 149 days (Table 1).

We chose trap arrays in TYE and TYW based on the extent of tiger habitat available after discounting nearly 27–35 % of the reserve areas that were heavily impacted by human settlements. Surveys in TYE and TYW could not be conducted in each year due to resource constraints in the initial years of study. Thus, surveys in TYE consisted of a total of 11 primary periods sampling 33–45 locations over 37–60 days covering trap array areas of 215–295 km^2. In TYW, trap array sizes were 166–176 km^2 with 30–45 camera traps deployed over 36–66 days during 12 primary sampling periods (Table 1; Fig. 2).

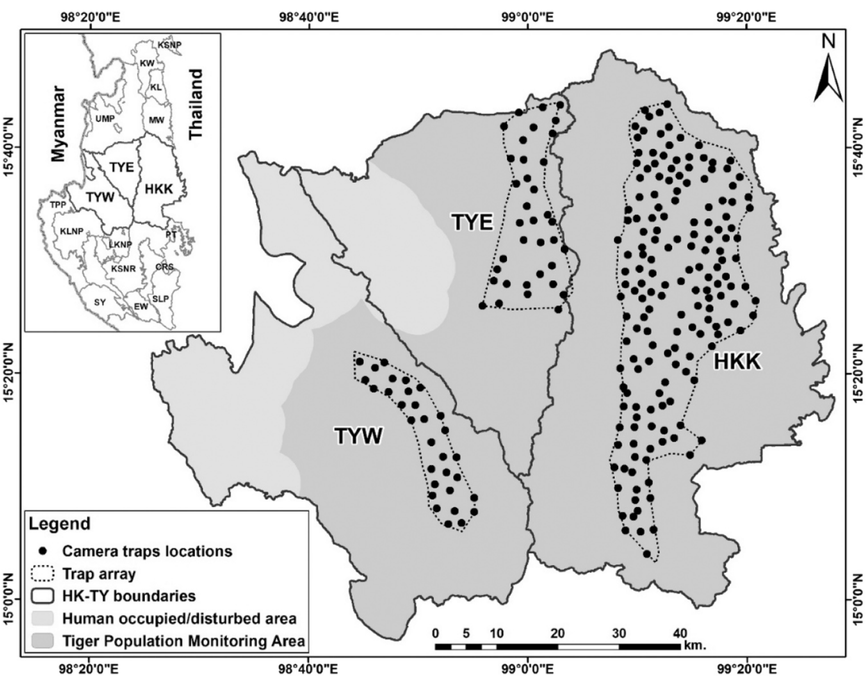

Fig. 2. Camera-trap locations in Huai Kha Khaeng (HKK), Thung Yai East (TYE) and Thung Yai West (TYW) Wildlife Sanctuaries together cover about 5,300 km^2 of WEFCOM area (in dark gray) during the long-term population monitoring from 2007 to 2023. The inset map shows the location of the study area within WEFCOM.

2.3. Analytical methods

2.3.1. Tiger density and abundance estimation

We used software program *ExtractCompare* (Hiby et al., 2009) to rapidly identify individual tigers from camera trap photos. All CR analyses were restricted to images of tigers judged to be >1 year old (Karanth and Nichols, 1998). Because our sampling conducted during dry season straddled two successive calendar years, primary periods were identified by the second calendar year (e.g., primary period 2023 refers to the sampling between November 2022 and February 2023). Within each primary period, we identified each calendar day as the secondary sampling period.

To estimate tiger density and abundance within each primary period, we relied on closed spatial capture-recapture (SCR) model (Royle et al., 2014; Royle et al., 2017) that accounts for heterogeneity in capture probability arising from variable trap exposure. The model explicitly incorporates animal location and movement data into the modeling, thus avoiding uncertainties involved in estimating densities from abundance obtained from non-spatial CR models. The spatiotemporal investment of trapping effort in each sampling occasion was specified by the trap deployment matrix input file, which included information on trap locations (latitude and longitude) and whether any trap was active (1) or inactive (0) on each secondary occasion. We estimated the following season-specific population parameters: tiger density $\widehat{D}$ (100 km^{-2}), basal trap encounter rate $\widehat{\lambda}_0$, movement parameter $\widehat{\sigma}$ and the probability that a member of the data-augmented population M is a real tiger $\widehat{\psi}$ (Royle et al., 2014).

Based on the results of earlier studies (Duangchantrasiri et al., 2016), we defined the discrete state-space S for each trap array by establishing a buffer distance of 15 km. We also deleted habitat patches within the identified state-space, such as larger human settlements or reservoirs that could not contain activity centers of individual tigers. We augmented the data on number of tigers captured each season n by 6 times to represent the maximum number of individual tigers M that could potentially occur within state-space S (Gopalaswamy et al., 2012).

Although there are differences in tiger movements and space-use between sexes, we used an intercept-only model $\lambda_0(.), \sigma(.)$ for drawing inference on parameters λ_0 and σ since we expected the three additional parameters (assuming females are coded 0 and males 1, as is the convention: an offset for males for λ_0, and offset for males for σ, and a mixing parameter to accommodate those individuals whose sex is unknown) required for modeling sex-specific differences to lead to non-convergence of Markovian Chains in several datasets due to sample-size constraints, which was the case in our study. Also, because $\widehat{\lambda}_0$ and $\widehat{\sigma}$ are inversely related (an animal that ranges more widely must necessarily spend less time in a specific location, unless proportion of time active also proportionally increases with ranging), we expected compensatory heterogeneity (Efford and Mowat, 2014) to minimize much of the bias (e.g. in $\widehat{D}$) due to heterogeneity in $\widehat{\lambda}_0$ and $\widehat{\sigma}$.

All analyses were implemented using the program SPACECAP (Gopalaswamy et al., 2012). We initially ran MCMC algorithm through 52,000 iterations with 2,000 burn-in. Based on Geweke statistic ($|$z-score$|>1.6$), examination of trace plots and kernel density plots (Royle et al., 2017), we re-analyzed datasets increasing burn-in to 20,000 and selecting results from subsequent 50,000 iterations, without thinning. A couple of datasets with very few individual captures and recaptures had to be further re-analyzed for 200,000 iterations (with 50,000 burn-in) to achieve MCMC convergence. We computed Monte Carlo simulation errors of all estimated parameters using the R package mcmcse (Flegal et al., 2021) to additionally assess reliability of posterior estimates (Dorazio, 2016).

We multiplied tiger density estimates by sampled area to derive season-specific abundance estimates. In HKK, season-specific abundance was derived for the entire reserve (2,780 km^2); while in TYE and TYW abundance was estimated for 1,095 km^2 and 1,425 km^2, respectively, that excluded heavily human-impacted areas. These expected abundances ($\widehat{N}$) were used to compute interval-specific numbers of recruits.

2.3.2. Estimation of tiger population dynamic parameters

Because spatial CR models currently available for open population analyses are sensitive to specification of state-space as well as model describing dynamics of activity centers (Gardner et al., 2018), we used a two-step analytical approach followed by Duangchantrasiri et al., (2016) to derive estimates of tiger population dynamic parameters (Pollock, 1982). We used likelihood-based Cormack-Jolly-Seber (CJS) models (Cormack, 1964; Jolly, 1965; Seber, 1965) implemented in program MARK (White and Burnham, 1999) to estimate probabilities of recapture and survival across multiple primary periods. Thereafter, we estimated recruitment and population growth rates by combining parameter estimates from both open non-spatial and closed SCR model analyses.

To enable valid inference on recruitment and population change rate, only data from a fixed trap array were used. Therefore, HKK survey data from 2005 and 2006 period, which employed smaller trap arrays, were excluded. The trap array sizes were fixed at 991-km^2 area first surveyed during 2007 for HKK, 295-km^2 area first surveyed in 2008 for TYE, and 176-km^2 area first surveyed in 2007 for TYW. However, for estimating survival, we included all capture history data that were available for estimating survival rates. We note that apparent survival is sensitive to variations in study area changes. However, as the trap array size becomes larger, fewer individuals are lost from the population to permanent emigration. In such cases, apparent survival estimate becomes closer to true survival (as its complement does not include movement), which may cause comparisons between early and late survival estimates to be potentially biased.

We fitted four plausible CJS models (Cormack, 1964; Jolly, 1965; Seber, 1965) to multi-year capture histories in each site, where apparent survival parameter φ and recapture probability p were treated as either constant or variable over time. Apparent survival φ_t is the probability that an individual alive and within the population at time t survives and remains in the population at time t+1, and its complement 1- φ_t includes both mortality and permanent emigration. Recapture probability p_t is the probability that a marked (previously photographed) animal alive and in the population at occasion t is captured or photographed during occasion t.

We assessed support for each proposed model from our data using Akaike's Information Criterion, corrected for small sample sizes (AICc; Burnham and Anderson, 2002). Annualized survival rate estimates $\widehat{\varphi}_t$ generated by program MARK were converted to interval-specific survival rate estimates $\widehat{\varphi}_t^{\Delta t}$ for subsequent estimation of derived parameters.

We combined CJS estimates of interval-specific survival probabilities with season-specific abundance estimates from closed SCR analyses (Duangchantrasiri et al., 2016) to derive expected number of recruits ($\widehat{B}_t = \widehat{N}_{t+1} - \widehat{\varphi}_t^{\Delta t}\widehat{N}_t$), per-capita annual recruitment rate $\left(\widehat{f}_t = \widehat{\lambda}_t^{\frac{1}{\Delta t}} - \widehat{\varphi}_t\right)$, interval-specific population change rates ($\widehat{\lambda}_t = \widehat{N}_{t+1}/\widehat{N}_t$), annualized population change rates $\widehat{\lambda}_t^{\frac{1}{\Delta t}}$ and overall change in mean abundance $\widehat{\overline{\lambda}}$ at each study site (HKK: 2007–2023; TYE: 2008–2023; TYW: 2007–2023). As all analyses were restricted to individuals >1 year age, the expected number of recruits $\widehat{B}_t$ is composed of individuals >1 year of age that immigrate into each of the three PAs, and individuals that are born within the PA and survive the first 12 months (rather than just immigration and births, as recruitment is usually interpreted). Variances of interval-specific, annualized and overall geometric mean rate of population change were calculated using the delta method approximation (Powell, 2007).

Because assessment of changes in population over time is confounded by sampling variance, we estimated true temporal variation in density following Link and Nichols (Link and Nichols, 1994) to separate signal from noise.

Table 2

Estimates of season-specific tiger density $\widehat{D}$, movement parameter $\widehat{\sigma}$, basal encounter rate $\widehat{\lambda}_0$, and the probability that a member of the data-augmented population is a real tiger $\widehat{\psi}$, along with posterior standard deviations (all parameters) and 95 % credible interval (tiger density), from camera trap surveys of tigers in Huai Kha Khaeng (2004/2005–2023), Thung Yai East (2008–2023) and Thung Yai West (2007–2023) in WEFCOM, Thailand. *Estimates in *italics* may be unreliable due to non-convergence of the Markov chain.

Site	Season	$\widehat{\sigma}$ ($\widehat{SD}$), km	$\widehat{\lambda_0}$($\widehat{SD}$)	$\widehat{\psi}$($\widehat{SD}$)	$\widehat{D}$($\widehat{SD}$), 100 km^{-2}	$\widehat{D}$ 95 % CI
HKK	2004–2005	4.080 (0.38)	0.050 (0.007)	0.483 (0.10)	1.82 (0.35)	1.19–2.53
	2006	3.424 (0.37)	0.020 (0.004)	0.545 (0.11)	2.09 (0.39)	1.33–2.81
	2007	4.357 (0.46)	0.015 (0.003)	0.368 (0.07)	1.45 (0.25)	1.00–1.95
	2008	5.305 (0.44)	0.016 (0.002)	0.292 (0.05)	1.49 (0.22)	1.06–1.88
	2009	6.375 (0.63)	0.009 (0.002)	0.298 (0.06)	1.39 (0.22)	1.00–1.84
	2010	3.562 (0.30)	0.026 (0.004)	0.372 (0.07)	1.63 (0.26)	1.13–2.10
	2011	6.373 (0.59)	0.011 (0.002)	0.264 (0.05)	1.31 (0.19)	1.00–1.71
	2012	3.506 (0.23)	0.022 (0.003)	0.399 (0.06)	2.05 (0.30)	1.47–2.62
	2013	4.609 (0.34)	0.018 (0.003)	0.323 (0.05)	1.76 (0.24)	1.30–2.23
	2014	3.974 (0.29)	0.021 (0.003)	0.362 (0.06)	1.91 (0.28)	1.36–2.43
	2015	6.146 (0.41)	0.017 (0.002)	0.243 (0.04)	1.39 (0.17)	1.06–1.69
	2016	4.063 (0.29)	0.025 (0.004)	0.338 (0.06)	1.58 (0.23)	1.15–2.04
	2017	3.056 (0.12)	0.037 (0.003)	0.353 (0.05)	2.46 (0.29)	1.88–2.99
	2018	4.244 (0.19)	0.025 (0.002)	0.282 (0.04)	1.74 (0.20)	1.34–2.10
	2019	3.442 (0.14)	0.029 (0.003)	0.324 (0.05)	2.21 (0.25)	1.73–2.71
	2020	3.417 (0.13)	0.035 (0.003)	0.321 (0.05)	2.09 (0.24)	1.60–2.53
	2021	3.229 (0.11)	0.040 (0.003)	0.326 (0.04)	2.32 (0.26)	1.86–2.86
	2022	3.376 (0.13)	0.035 (0.003)	0.321 (0.04)	2.57 (0.27)	2.04–3.05
	2023	3.396 (0.13)	0.030 (0.002)	0.326 (0.04)	2.86 (0.29)	2.30–3.42
TYE	2008	9.537 (2.27)	0.039 (0.017)	0.193 (0.08)	0.23 (0.06)	0.19–0.34
	2011*	*15.305 (21.51)*	*0.013 (0.011)*	*0.461 (0.25)*	*0.49 (0.27)*	*0.15–0.99*
	2013	6.034 (1.38)	0.039 (0.020)	0.287 (0.13)	0.44 (0.18)	0.23–0.80
	2015	9.440 (3.19)	0.027 (0.014)	0.225 (0.13)	0.16 (0.08)	0.11–0.34
	2017	11.275 (8.41)	0.012 (0.006)	0.229 (0.11)	0.28 (0.12)	0.19–0.53
	2018	5.128 (0.61)	0.028 (0.006)	0.299 (0.08)	1.02 (0.24)	0.61–1.49
	2019	3.909 (0.32)	0.047 (0.008)	0.359 (0.10)	0.94 (0.24)	0.53–1.41
	2020	4.668 (0.58)	0.039 (0.009)	0.310 (0.10)	0.73 (0.20)	0.42–1.14
	2021	4.019 (0.41)	0.061 (0.016)	0.349 (0.11)	0.83 (0.23)	0.42–1.26
	2022	5.864 (0.53)	0.069 (0.026)	0.207 (0.05)	0.86 (0.15)	0.61–1.14
	2023	3.810 (0.31)	0.070 (0.012)	0.342 (0.07)	1.81 (0.34)	1.22–2.51
TYW	2007	5.284 (0.18)	0.022 (0.010)	0.497 (0.20)	0.89 (0.34)	0.33–1.57
	2010	7.340 (0.25)	0.033 (0.018)	0.314 (0.16)	0.31 (0.16)	0.15–0.62
	2012*	*64.207 (59.12)*	*0.004 (0.012)*	*0.541 (0.25)*	*0.42 (0.20)*	*0.15–0.77*
	2014	5.285 (0.71)	0.211 (0.168)	0.268 (0.11)	0.39 (0.13)	0.22–0.66
	2016	4.150 (0.58)	0.044 (0.010)	0.458 (0.14)	1.04 (0.31)	0.47–1.64
	2017	9.834 (2.34)	0.023 (0.010)	0.212 (0.10)	0.20 (0.07)	0.15–0.33
	2018	4.839 (0.55)	0.047 (0.011)	0.388 (0.16)	0.39 (0.15)	0.15–0.69
	2019	4.645 (0.56)	0.028 (0.006)	0.400 (0.13)	0.91 (0.27)	0.44–1.42
	2020	4.457 (0.88)	0.036 (0.010)	0.460 (0.18)	0.70 (0.27)	0.22–1.20
	2021	4.050 (0.56)	0.044 (0.010)	0.481 (0.16)	1.10 (0.34)	0.47–1.75
	2022	3.818 (0.39)	0.041 (0.009)	0.498 (0.17)	0.76 (0.25)	0.36–1.31
	2023	2.520 (0.21)	0.048 (0.008)	0.748 (0.14)	3.07 (0.56)	2.12–4.09

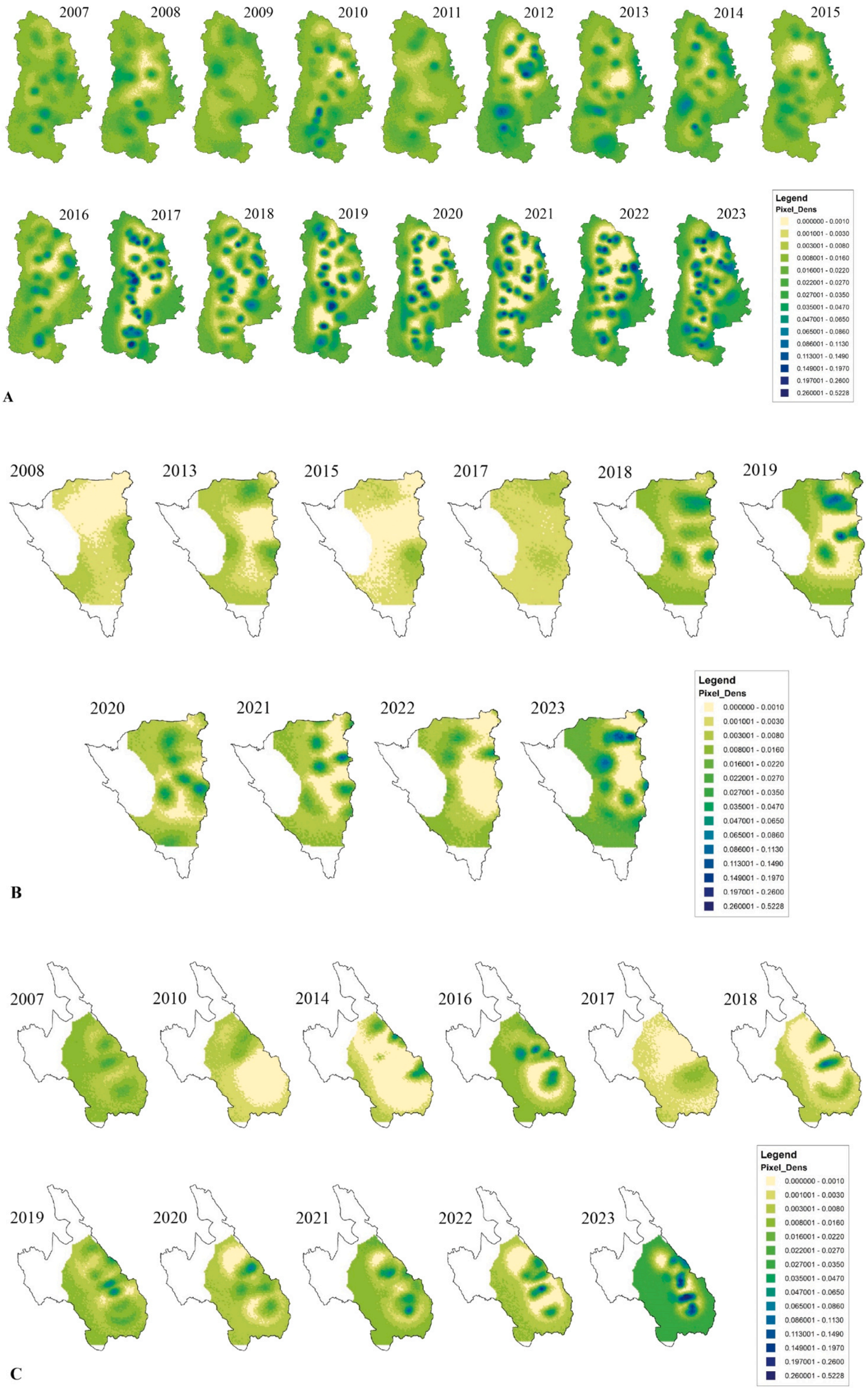

Fig. 3. Estimated fine-scale spatial pattern of tiger densities per 0.336 km^2 pixel, generated with program SPACECAP, for Huai Kha Khaeng 2007–2023 (A), Thung Yai East 2008–2023 (B), and Thung Yai West 2007–2023 (C). Darker colors (blue) correspond to higher densities, while lighter colors (yellow) indicate lower densities.

3. Results

Summary details of camera trap surveys in HKK-TY during 2005–2023 are presented in Table 1. Cumulatively, we expended 98,305 trap-days of sampling effort across the three sites between 2005 and 2023 (72,470 in HKK; 13,040 in TYE; 12,795 trap-days in TYW). This most extensive, long-term camera trap-based study of tigers in southeast Asia resulted in photo-captures of 291 individuals of >1 year of age during the entire study period (211 in HKK, 47 in TYE and 43 in TYW, with 10 individuals photo-captured in more than one PA). Photo-captures of 67 tigers (43 from HKK, 14 from TYE and 10 from TYW) judged to be of <1 year of age at the time of capture were excluded from analyses.

Estimates of tiger abundance and other parameters obtained from closed SCR analyses are presented in Table 2. Close examination of MCMC diagnostics showed convergence in all datasets except for the two datasets in TYE 2011 and TYW 2012, wherein a few parameters failed to converge to stationary distributions due to low sample-sizes (very few individuals and recaptures). Hence, parameter estimates from TYE 2011 and TYW 2012 datasets are likely to be unreliable and are marked in *italic font* (see Table 2). Excluding parameter estimates from analyses that did not achieve convergence, tiger densities/100 km^2 ($\widehat{D}$ [±posterior SD; primary period]) ranged from 1.3 (0.19; 2011) to 2.9 (0.29; 2023) in HKK between 2007 and 2023, from 0.2 (0.08; 2015) to 1.8 (0.34; 2023) in TYE between 2008 and 2023, and from 0.2 (0.07; 2017) to 3.1 (0.56; 2023) in TYW between 2007 and 2023, clearly showing an overall increase in tiger densities at all the three sites after increasing protection since 2007. Estimated movement parameter values in km ($\widehat{\sigma}$, [±posterior SD; primary period]) ranged from 3.1 (0.12; 2017) to 6.4 (0.63; 2009) in HKK, from 3.8 (0.31; 2023) to 11.3 (8.41; 2017) in TYE, and from 2.5 (0.21; 2023) to 9.8 (2.34; 2017) in TYW. Spatial and temporal variation in tiger densities in HKK-TY, at the scale of 0.336 km^2 pixels, is shown in Fig. 3.

Model selection results from open population analyses conducted for HKK-TY are presented in Table 3. The CJS model with constant survival and constant recapture probabilities {φ(.), p(.)} received unequivocal support in all three sites and was used for all subsequent inference. Estimates of annual survival $\widehat{\varphi}(\widehat{SE})$ and other vital rates together with season-specific tiger abundance $\widehat{N_t}$ in HKK-TY are provided in Table 4. Unreliable estimates of $\widehat{N}_t$, $\widehat{B}_t$, and $\widehat{\lambda}_t^{\frac{1}{\Delta t}}$ derived from analyses that failed to converge are marked in *italics*. Annual survival $\widehat{\varphi}(\widehat{SE})$ was highest in HKK [0.79 (0.02)] as compared to TYE [0.72 (0.05)] and TYW [0.69 (0.05)]. In HKK, interval-specific annual recruitment rate $\widehat{\widehat{f}}_t(\widehat{SE})$ ranged from -0.08 (SE 0.37) in 2017 to 0.77 (SE 0.56) in 2016 over the 2007–2023 period. In contrast, per-capita recruitment rate in TYE ranged from -0.12 (SE 0.50) in 2013 to 2.0 (SE 1) in 2017, and from -0.48 (SE 0.37) in 2016 to 3.49 (SE 1.29) in 2022 in TYW.

In HKK, annualized fluctuations in estimated tiger densities ($\widehat{\lambda}_t^{\frac{1}{\Delta t}}$) between 2007 and 2023 were substantial ranging from 0.71 (0.12; i.e. 29 % decline) to 1.56 (0.30; 56 % increase), in contrast to extreme inter-annual fluctuations in TYE and TYW. In TYE, annualized finite rate of population change ranged from 0.60 (0.20; 40 % decline) to 2.72 (0.96; 172 % increase) between 2008 and 2023, while in TYW it ranged from 0.21 (0.09; 79 % decline) to 4.18 (1.60; 318 % increase) during 2007–2023.

Overall, the geometric mean of annual population change $\widehat{\widehat{\lambda}}(SE)$ in HKK was 1.04 (0.01) or 4 % mean annual growth sustained over 2007–2023, in contrast to 1.14 (0.03) in TYE (i.e., mean annual increase of 14 % sustained over 2008–2023), and 1.08 (0.03) in TYW (mean annual increase of 8 % over 2007–2023).

4. Discussion

4.1. Elements of effective tiger population recoveries in tropical Asia

Although the present study focuses on a tiger recovery in Thailand measured only after 2007, it must be viewed in the overall context of massive historical range contractions and widespread extirpations of tigers across tropical Asia by the 1960s (Walston et al., 2010; Goodrich et al., 2022). Because of resultant global conservation concerns, policies were promulgated after the 1970s in most

Table 3
Model selection results from CJS analyses of multi-year capture histories of adult tigers in Huai Kha Khaeng (2004/2005–2023), Thung Yai East (2008–2023) and Thung Yai West (2007–2023) in WEFCOM, Thailand. Boldface font indicates the minimum AIC model for each dataset.

Site	Model	No. of parameters	AICc	Δ AICc	AICc weight
HKK	***{phi(.),p(.)}***	**2**	**1000.95**	**0**	**0.9977**
	{phi(t),p(.)}	19	1013.45	12.50	0.0019
	{phi(.),p(t)}	19	1017.00	16.04	0
	{phi(t),p(t)}	35	1028.08	27.13	0
TYE	***{phi(.),p(.)}***	**2**	**104.77**	**0**	**0.9567**
	{phi(t),p(.)}	11	110.99	6.22	0.0426
	{phi(.),p(t)}	11	119.53	14.76	0
	{phi(t),p(t)}	17	125.64	20.87	0
TYW	***{phi(.),p(.)}***	**2**	**98.96**	**0**	**0.9987**
	{phi(.),p(t)}	12	113.42	14.46	0
	{phi(t),p(.)}	12	114.02	15.05	0
	{phi(t),p(t)}	21	136.55	37.58	0

Table 4

Estimates of season-specific expected abundance $\widehat{N_t}$, recapture probability $\widehat{p}_t$, interval-specific annual survival $\widehat{\varphi}_t$, interval survival $\widehat{\varphi}_t{}^{\Delta t}$, interval recruitment $\widehat{B}_t$, interval-specific annual recruitment rate $\widehat{f}_t$, and annualised rate of population change $\widehat{\lambda}_t^{\frac{1}{\Delta t}}$ with associated standard errors, from Huai Kha Khaeng (2004/2005–2023), Thung Yai East (2008–2023) and Thung Yai West (2007–2023) in WEFCOM, Thailand. *Estimates in italics ($\widehat{N}_t$, $\widehat{B}_t$, $\widehat{\lambda}_t^{\frac{1}{\Delta t}}$) may be unreliable due to non-convergence of the Markov chain.

Site	Season	$\widehat{N_t}$ ($\widehat{SE}$)	$\widehat{p}$ ($\widehat{SE}$)	$\widehat{\varphi}$ ($\widehat{SE}$)	$\varphi_t{}^{\Delta t}$($\widehat{SE}$)	$\widehat{B_t}$ ($\widehat{SE}$)	$\widehat{f}_t$ ($\widehat{SE}$)	$\widehat{\lambda}_t^{\frac{1}{\Delta t}}$($\widehat{SE}$)
HKK	2004–2005	-	-	0.79 (0.016)	0.72 (0.017)	-	-	-
	2006	-	0.90 (0.015)	0.79 (0.016)	0.78 (0.016)	-	-	-
	2007	40.31 (1.32)	0.90 (0.015)	0.79 (0.016)	0.79 (0.016)	9.60 (1.68)	0.24 (0.496)	1.03 (0.23)
	2008	41.42 (1.16)	0.90 (0.015)	0.79 (0.016)	0.81 (0.016)	5.21 (1.62)	0.14 (0.465)	0.93 (0.20)
	2009	38.64 (1.16)	0.90 (0.015)	0.79 (0.016)	0.77 (0.016)	15.32 (1.75)	0.38 (0.506)	1.17 (0.24)
	2010	45.31 (1.37)	0.90 (0.015)	0.79 (0.016)	0.79 (0.016)	0.40 (1.64)	0.01 (0.443)	0.80 (0.18)
	2011	36.42 (1.00)	0.90 (0.015)	0.79 (0.016)	0.79 (0.016)	28.26 (1.86)	0.77 (0.58)	1.56 (0.32)
	2012	56.99 (1.58)	0.90 (0.015)	0.79 (0.016)	0.79 (0.016)	3.79 (2.00)	0.07 (0.431)	0.86 (0.17)
	2013	48.93 (1.27)	0.90 (0.015)	0.79 (0.016)	0.80 (0.016)	14.18 (1.94)	0.29 (0.486)	1.09 (0.22)
	2014	53.10 (1.48)	0.90 (0.015)	0.79 (0.016)	0.79 (0.016)	0 (1.69)	-0.06 (0.395)	0.73 (0.14)
	2015	38.64 (0.90)	0.90 (0.015)	0.79 (0.016)	0.79 (0.016)	13.35 (1.53)	0.35 (0.486)	1.14 (0.22)
	2016	43.92 (1.21)	0.90 (0.015)	0.79 (0.016)	0.79 (0.016)	33.48 (1.93)	0.77 (0.562)	1.56 (0.30)
	2017	68.39 (1.53)	0.90 (0.015)	0.79 (0.016)	0.82 (0.015)	0 (1.93)	-0.08 (0.367)	0.71 (0.12)
	2018	48.37 (1.05)	0.90 (0.015)	0.79 (0.016)	0.79 (0.016)	23.13 (1.73)	0.48 (0.465)	1.27 (0.20)
	2019	61.44 (1.32)	0.90 (0.015)	0.79 (0.016)	0.79 (0.016)	9.39 (1.90)	0.16 (0.407)	0.95 (0.15)
	2020	58.10 (1.27)	0.90 (0.015)	0.79 (0.016)	0.79 (0.016)	18.64 (1.93)	0.32 (0.443)	1.11 (0.18)
	2021	64.50 (1.37)	0.90 (0.015)	0.79 (0.016)	0.79 (0.016)	20.39 (2.05)	0.32 (0.431)	1.11 (0.17)
	2022	71.44 (1.42)	0.90 (0.015)	0.79 (0.016)	0.79 (0.016)	22.86 (2.20)	0.32 (0.42)	1.11 (0.16)
	2023	79.41 (1.53)	0.90 (0.015)	-	-	-	-	-
TYE	2008	2.52 (0.21)	-	0.72 (0.048)	0.38 (0.043)	4.42 (0.90)	0.57 (0.55)	1.29 (0.26)
	2011*	*5.37 (0.89)*	0.97 (0.034)	0.72 (0.048)	0.52 (0.049)	*2.02 (0.80)*	*0.23 (0.61)*	*0.95 (0.32)*
	2013	4.82 (0.60)	0.97 (0.034)	0.72 (0.048)	0.52 (0.049)	0 (0.47)	-0.12 (0.5)	0.60 (0.20)
	2015	1.75 (0.26)	0.97 (0.034)	0.72 (0.048)	0.52 (0.048)	2.05 (0.40)	0.57 (0.68)	1.29 (0.41)
	2017	2.96 (0.36)	0.97 (0.034)	0.72 (0.048)	0.65 (0.049)	9.25 (0.84)	2.00 (1)	2.72 (0.96)
	2018	11.17 (0.79)	0.97 (0.034)	0.72 (0.048)	0.72 (0.048)	2.20 (1.12)	0.2 (0.61)	0.92 (0.32)
	2019	10.29 (0.79)	0.97 (0.034)	0.72 (0.048)	0.72 (0.048)	0.57 (1.01)	0.06 (0.58)	0.78 (0.29)
	2020	7.99 (0.66)	0.97 (0.034)	0.72 (0.048)	0.72 (0.048)	3.32 (1.28)	0.42 (0.7)	1.14 (0.44)
	2021	9.09 (0.76)	0.97 (0.034)	0.72 (0.048)	0.72 (0.048)	2.86 (0.70)	0.32 (0.62)	1.04 (0.34)
	2022	9.42 (0.50)	0.97 (0.034)	0.72 (0.048)	0.73 (0.047)	12.98 (0.57)	1.41 (0.78)	2.13 (0.56)
	2023	19.82 (4.45)	0.97 (0.034)	-	-	-	-	-
TYW	2007	12.68 (1.28)	-	0.69 (0.050)	0.34 (0.042)	0.15 (0.92)	0.01 (0.447)	0.70 (0.15)
	2010	4.42 (0.60)	0.96 (0.040)	0.69 (0.050)	0.48 (0.049)	3.88 (0.84)	0.47 (0.67)	1.16 (0.40)
	2012*	*5.99 (0.75)*	0.96 (0.040)	0.69 (0.050)	0.48 (0.049)	*2.69 (0.68)*	*0.27 (0.574)*	*0.96 (0.28)*
	2014	5.56 (0.49)	0.96 (0.040)	0.69 (0.050)	0.48 (0.049)	12.14 (1.23)	0.95 (0.647)	1.64 (0.37)
	2016	14.82 (1.17)	0.96 (0.040)	0.69 (0.050)	0.68 (0.051)	0 (1.13)	-0.48 (0.375)	0.21 (0.09)
	2017	2.85 (0.26)	0.96 (0.040)	0.69 (0.050)	0.63 (0.051)	3.77 (0.61)	1.00 (0.861)	1.69 (0.69)
	2018	5.56 (0.57)	0.96 (0.040)	0.69 (0.050)	0.69 (0.050)	9.11 (1.13)	1.64 (1.086)	2.33 (1.13)
	2019	12.97 (1.02)	0.96 (0.040)	0.69 (0.050)	0.69 (0.050)	0.97 (1.40)	0.08 (0.656)	0.77 (0.38)
	2020	9.98 (1.02)	0.96 (0.040)	0.69 (0.050)	0.70 (0.050)	8.74 (1.55)	0.89 (0.911)	1.58 (0.78)
	2021	15.68 (1.28)	0.96 (0.040)	0.69 (0.050)	0.69 (0.050)	0.06 (1.52)	0.01 (0.6)	0.70 (0.31)
	2022	10.83 (0.94)	0.96 (0.040)	0.69 (0.050)	0.70 (0.050)	36.18 (2.28)	3.49 (1.288)	4.18 (1.61)
	2023	43.75 (2.11)	0.96 (0.040)	-	-	-	-	-

tropical Asian countries to enhance protection of tiger populations and their habitats. However, the effective implementation of such protective measures on ground was sporadic and restricted to a few reserves in India and Nepal. Over most of southeast Asia, tiger declines continued, leading to extirpation of tigers from Java in late 1970s, as well as from Cambodia, Lao, and Viet Nam by the mid-2000s. Tigers now survive only in small, isolated populations in Sumatra, Peninsular Malaysia, Myanmar, and Thailand.

However, within the WEFCOM region of Thailand, as far back as in 1970s, substantial village resettlement projects were taken up in HKK-TY to stem forest fragmentation and encroachments. These foundational conservation interventions included relocation of Karen and Thai villages from HKK in mid-1970s and of Hmong settlements from TYE in 1990s (Voravann, 2017), and closure of intensive mining activity in TYW in early 1990s. These habitat consolidation measures provided an isolated but extensive land-base for achieving modest tiger population recoveries, after anti-hunting measures were added to the arsenal of law-enforcement agencies (Simcharoen et al., 2007).

The poaching wave in the 2000s, driven by the newly emergent trade in tiger body parts in China, prompted the Thai Government to implement a focused, stronger system of anti-poaching patrols after 2006 (WCS Thailand, 2013; DNP, 2022b). These measures speeded up the tiger recovery first in HKK, as documented by Duangchantrasiri et al., (2016), followed by TYE and TYW (this study). Although these tiger recoveries were not at the same scale or intensity as observed in India (Karanth et al., 2020) and Nepal, they do provide a unique example of tiger recovery in southeast Asia driven by substantial habitat protection and anti-poaching efforts.

In contrast, there are no comparable examples of population recoveries documented in the absence of strong protection measures directed at tigers, their prey and habitats in tropical Asia. Indirect conservation measures such as community-based and livelihood-related interventions appear to contribute to tiger recoveries only when strong and direct protection efforts are also in place. When on-ground protection is ineffective and nominal, tiger recovery may fail as evidenced by their recent extirpations from Cambodia where substantial investments were made in both anti-poaching patrol and in-situ community support activities. A similar extirpation process appears to be now unfolding in the case of leopards in Cambodia (Rostro-García et al., 2023).

4.2. *Tiger ecology and population dynamics in WEFCOM*

From among all the tigers we photo-captured (291 individuals over one-year age), only 10 tigers had home ranges that straddled two study sites. We also note that among cubs <1 year age, 43 were detected in HKK, 14 in TYE, and 10 in TYW in the 2013–2023 period. These photo-capture histories suggest that each reserve supported distinct clusters of breeding tiger territories with only occasional exchanges of dispersing individuals (see Table 5).

The average annual tiger survival rates (79 % in HKK, 72 % in TYE and 69 % in TYW) were comparable to estimates reported from other studies (82% in HKK from an earlier study for 2005–2012, Duangchantrasiri et al., 2016; 77 % in Nagarahole, Karanth et al., 2006; 66 % in Pench, Majumder et al., 2017; 68 % in Corbett, Bisht et al., 2019; 81 % in Rajaji, Harihar et al., 2020). The tiger survival estimates in TYE and TYW were lower than in HKK plausibly due to shorter histories of protection, higher human impacts, and consequently lower densities of principal prey species in these two reserves (Duangchatrasiri et al., 2019; Jornburom et al., 2020). Nearly 27 % of the area in TYE and 35 % in TYW is impacted by anthropogenic activities originating from 16 villages (7 in TYE and 9 in TYW; average population size ~235) located in their northwestern parts, in stark contrast to HKK where the village relocation process was completed by mid-1970s (WEFCOM, 2004). Another contributing factor could be that these two populations were initially augmented through 'rescue effect' (Brown and Kodric-Brown, 1977) of tigers dispersing from HKK (see Table 5). Such rescued tiger populations may have lower survival rates because of preponderance of dispersing male tigers with lower survival rates. A third factor could be the contribution of a higher level of permanent emigration, compared to HKK, in the complement of apparent survival rates (1- φ_t) in TYE and TYW reserves.

In HKK, the mean population density fluctuated substantially between 1.3 and 2.9 tigers/100 km^2 during 2005–2023, as was observed in earlier studies (1.3–2.1 in HKK observed during 2005–2012, Duangchantrasiri et al., 2016; 7.3–21.7 in Nagarahole, Karanth et al., 2006; 3.1–5.5 in Pench, Majumder et al., 2017; 12–17 in Corbett, Bisht et al., 2019; 2.1–7.1 in Rajaji, Harihar et al., 2020). Even after accounting for sampling variance, which contributed to ~15 % of the total variance, the temporal variance in tiger densities in HKK was substantial (see Annexure A Supporting information). Such density fluctuations appear to be intrinsic to tiger populations because of demographic stochasticity (Pielou, 1969; Williams et al., 2002) arising mainly from varying numbers of resident females that breed in any given year (Karanth and Stith, 1999), and environmental stochasticity (May, 1974). The chance synchrony in gains and losses of tigers due to other factors is also likely to contribute to such fluctuations.

Population density fluctuations in TYE (0.2–1.8 tigers/100 km^2) and TYW (0.2–3.1 tigers/100 km^2) were higher than in HKK, possibly because smaller tiger populations are impacted to a greater degree by demographic stochasticity (Pielou, 1969; Karanth and Stith, 1999). We also note the relatively greater variation in mean tiger abundances in these two reserves in successive years (a 318 % increase in TYW between 2022 and 2023; a 80 % decline in TYW between 2016 and 2017; see Table 4). Such drastic fluctuations are possible only in very small populations. For example, the massive tripling of the tiger population in TYW from 2022 to 2023 resulted from the estimated recruitment of 36 new individuals into the population. Nonetheless, such large numbers of recruits are unlikely to be sustained or even retained over longer periods in wild tiger populations. The standard deviation of the true temporal variation after correcting for sampling variation in the density estimates of the three study sites shows that tiger populations in TYE and TYW are more variable than in HKK ($\tau = 0.43$ in TYE and $\tau = 0.39$ in TYW vs $\tau = 0.14$ in HKK; see Fig. 5; Annexure A). These results emphasize the

Table 5
Dispersal movements by tigers among the Protected Areas in WEFCOM, Thailand from 2014 to 2023.

	2014–2023	Dispersal from									
		Huai Kha Khaeng	Thung Yai East	Thung Yai West	Mae Wong	Klong Lan	Khuean Srinagarindra	Salakpra	Khao Laem	Erawan	Phu Toei
Dispersal to	Huai Kha Khaeng		5	1	3		1				1
	Thung Yai East	8		2	1				1		
	Thung Yai West	3	2				1		2	1	
	Mae Wong	5	1								
	Klong Lan	2									
	Khuean Srinagarindra	1									
	Salakpra	3		1							
	Khao Laem	2									
	Erawan										
	Phu Toei										

Source: DNP. (DNP, 2023). An annual report of Khao Nang Ram Wildlife Research Station, Department of National Parks, Wildlife, and Plant Conservation, Bangkok, Thailand (In Thai).

risks of interpreting 'changes' in population size/density based on just a few years of density/abundance estimates, often ignoring their sampling variances (Link and Nichols, 1994).

The tiger population size in HKK (with its longer history of protection), grew at an annual rate of 4 %. This recovery appears to have influenced dispersal of at least 24 individual tigers into other populations within WEFCOM (Table 5). However, such dispersals, especially of male tigers, away from source populations, have been recorded in India even when the population density was lower than the density ultimately attained (Patil et al., 2011). Such dispersal behaviors in tigers are likely to be partially density-independent and rooted in their territorial social organization.

Changes in tiger abundances over time in TYE and TYW might also be artefacts of spatial shifts in the activity centers of individual tigers, in addition to other demographic factors. The fine-scale spatial patterns of tiger densities in TYE and TYW (Figs. 3B, 3C) do indicate such range shifts occurring in earlier years and increase in abundances during subsequent years. Furthermore, such population fluctuations are likely to be accentuated if transient tigers constitute a higher proportion of the small population.

Despite these population fluctuations and higher rate of annual losses of tigers, all three study populations showed an overall increasing growth rate (Fig. 5). Over a 16-year interval, the mean tiger population size grew at an average annual rate of 4 % in HKK, and a higher rate in TYE (14 %) and TYW (8 %). It is likely that the populations in the latter two areas were bolstered by several tiger dispersals from HKK and other reserves (Table 5).

A source population site at higher tiger density typically has a high reproduction rate contributing to both retentions and emigrations (Runge et al., 2006). Out of the 47 dispersal events documented in WEFCOM (Table 5), HKK-TY together accounted for ~77 % and a further ~45 % of them occurred among the three study sites. Rest of the events (23 %) were from five other protected areas, which clearly show HKK-TY as a stronghold for sustaining tiger populations in WEFCOM.

Establishment of new source populations in WEFCOM would eventually depend on movement of female tigers to new sites with sufficient prey densities to enable breeding and reproduction (Karanth et al., 2004). In WEFCOM, dispersal of eight female tigers from HKK to other protected areas were recorded. These include a female that dispersed to Mae Wong (MW) National Park, which successfully produced cubs later (Phumanee et al., 2021). More female dispersals have been recorded in other protected areas in WEFCOM (DNP, 2022a).

Above observations, together with the population-dynamic data from this study, provide evidence for habitat permeability that exists among key protected areas within WEFCOM, thus facilitating a source-sink dynamics within a functioning meta-population of tigers in the region. Furthermore, photo-capture records of 67 tiger cubs <1 year age in HKK-TY between 2013 and 2023, suggest that our study area supports one of the few demographically viable tiger source populations in southeast Asia. It can potentially be a key source for tiger population recoveries not only in the rest of WEFCOM but also in other contiguous forested landscapes from which tigers have been extirpated in recent decades. Overall, we submit that our estimates of tiger demographic parameters provide clear, quantitative evidence of robust population recoveries in all three sites within the WEFCOM, a conservation success rarely documented in the annals of tiger population management in Southeast Asia.

4.3. Tiger monitoring and management in WEFCOM: future direction

Given the iconic status of tigers in global conservation, many population surveys are being conducted across the tiger's range by governmental agencies. Among such efforts, tiger monitoring system established by the Government of Thailand in WEFCOM is unique because it was executed in collaboration with independent researchers from the Wildlife Conservation Society-Thailand (WCS), Kasetsart University (KU), Thailand and Centre for Wildlife Studies (CWS), India in a unique public-private partnership for monitoring populations of a charismatic species. This model stands in contrast to most tiger monitoring efforts under governmental monopolies that control survey design, implementation, data ownership, analyses, and outcomes.

We, however, believe the current monitoring system can be further improved to build on the impressive, documented tiger recoveries as proposed below:

(a) Long term studies using robust methodologies (Karanth et al., 2020; Harihar et al., 2020) show that both density and demographic viability of wild tiger populations depend primarily on density of large ungulate prey (30–1,000 kg body mass). These studies were conducted after the study areas had recovered their full complement of ungulate prey species at high densities, measured using rigorous line transect surveys. However, prey population assessment surveys in HKK-TY are only sporadic and the preliminary analyses show that densities of prey species such as sambar (*Rusa unicolor*) and banteng (*Bos javanicus*) have increased over the years, although others such as gaur (*Bos gaurus*) have not responded similarly (Saisamorn et al., 2024). We recommend initiating a rigorous monitoring system to estimate densities of principal prey using advanced line transect sampling methods (Dorazio et al., 2017; Kumar et al., 2021) to reliably identify ecological determinants of such recoveries.

(b) A large regional-level sign-based occupancy survey conducted in 2010–12 (Duangchatrasiri et al., 2019; Jornburom et al., 2020) showed the benchmark distribution of tigers and their prey across WEFCOM together with factors governing their occupancy patterns. Following significant conservation efforts invested across the region by the Thailand Government, it is necessary to evaluate local colonization and extinction patterns of tigers in WEFCOM. Camera-trap surveys and rigorous line transect surveys are not logistically and economically viable at large spatial scales (Karanth and Nichols, 2017). Therefore, we recommend conducting multi-year sign-based surveys to assess tiger and prey occupancy dynamics (Kumar et al., 2017) and prioritize potential sites for tiger-prey recolonization across the region.

Table 6
Details of spatial coverage, temporal frequency, and spatio-temporal index of foot-patrol efforts invested together with annual cumulative efforts and number of poacher camps encountered during 2007–2023 under SMART system in Huai Kha Khaeng (HKK), Thung Yai East (TYE) and Thung Yai West (TYW) sanctuaries in WEFCOM, Thailand (DNP, 2022b).

Year	Annual patrol effort (km)			Average patrol frequency / grid cell / year			Patrol coverage / year			Spatio-temporal index of patrol / year			No. of poacher camps detected / 1,000 km patrol		
	HKK	TYW	TYE	HKK	TYW	TYE	HKK	TYW	TYE	HKK	TYW	TYE	HKK	TYW	TYE
2007	7,424	0	96	2.38	0.00	0.06	59.56	0.00	6.47	141.9	0	0.4	3.64	0.00	0.00
2008	8,996	2,850	1,399	3.03	1.40	0.71	63.67	43.02	32.91	193	60.2	23.5	9.67	0.00	0.00
2009	11,027	6,993	3,996	3.58	3.42	1.94	63.92	66.56	54.73	228.6	227.3	106.3	4.90	0.43	4.00
2010	14,381	10,714	7,801	4.31	5.46	3.39	73.90	78.04	52.77	318.8	425.8	179	12.10	0.84	3.46
2011	15,793	10,073	10,200	4.56	4.84	4.32	78.91	69.27	68.51	359.5	335.3	295.9	7.79	0.89	4.12
2012	14,670	11,585	7,802	4.49	5.53	3.78	71.87	76.76	66.96	322.7	424.8	253.1	8.66	0.17	4.36
2013	16,920	11,860	8,361	4.88	5.68	3.58	71.18	83.06	61.11	347.7	472.1	218.6	6.09	0.42	3.35
2014	23,939	14,733	12,630	4.63	6.07	5.24	70.34	74.13	68.98	325.7	450.2	361.6	4.34	2.65	2.14
2015	23,633	14,858	12,789	5.37	5.94	5.36	76.46	78.34	65.51	410.6	465	350.9	3.09	2.49	2.50
2016	22,695	14,242	13,240	4.59	5.42	5.04	64.54	78.87	62.80	296	427.8	316.6	1.89	1.47	1.36
2017	21,621	16,340	13,721	4.62	5.79	5.42	68.25	82.52	78.75	315.3	478	426.8	2.64	2.20	1.31
2018	20,839	17,044	12,350	3.72	6.19	4.42	64.78	76.90	72.50	241	476.2	320.1	2.06	0.59	1.94
2019	25,738	13,340	12,213	4.43	5.04	4.29	76.16	72.52	74.07	337.7	365.7	317.8	1.55	2.17	1.72
2020	22,739	17,417	15,494	5.13	6.42	5.14	75.09	77.77	82.20	385	499	422.3	1.50	0.86	2.65
2021	19,186	18,254	13,212	4.34	6.32	4.74	73.39	80.66	74.03	318.3	509.4	350.9	1.51	0.66	1.82
2022	19,736	20,277	10,873	4.24	6.10	4.03	71.34	81.23	70.69	302.7	495.8	284.9	1.17	0.05	1.38
2023	16,001	19,176	9,611	4.37	6.10	4.39	73.57	81.09	72.92	321.5	494.3	320	1.19	0.31	1.98

4.4. Implications for effective tiger population recovery in tropical Asia

We submit that the core strategy of protecting tigers and their prey-base from local and market-driven hunting has been the critical component of the recovery we documented. The systematic deployment of armed foot-patrols, beginning in 2006 in HKK and thereafter extending the SMART patrol system to other areas of WEFCOM (DNP, 2022b) has expanded the scope of tiger recovery. Over the years, spatiotemporal coverages of the patrols have steadily increased, as evidenced by performance indicators that assess efficacy of protection to identify areas at highest risk from poachers (DNP, 2022b; see Table 6, Fig. 4). The resulting reduction in poaching activities is reflected in the lower number of encounter rates with poacher camps/1000 km of distance patrolled (Table 6). Furthermore, no instances of active tiger poaching were detected after 2013 (DNP, 2022b), despite increased protection efforts.

We note that similar outcomes have been achieved through stronger law-enforcement in India, Nepal, Russia, and other regions of tiger range (Karanth et al., 1999, 2020; Stokes, 2010; Linkie et al., 2015; DNPWC, 2016; Hotte et al., 2016). We also submit that the collaborative conservation monitoring implemented in HKK-TY provides a sound model for tiger monitoring range-wide, wherever appropriate management capacity can be created. Such an approach also appears relevant for accomplishing recoveries of other large predatory carnivores in Asia's fragmented habitats characterized by dense human populations, rapid economic growth and rising social aspirations.

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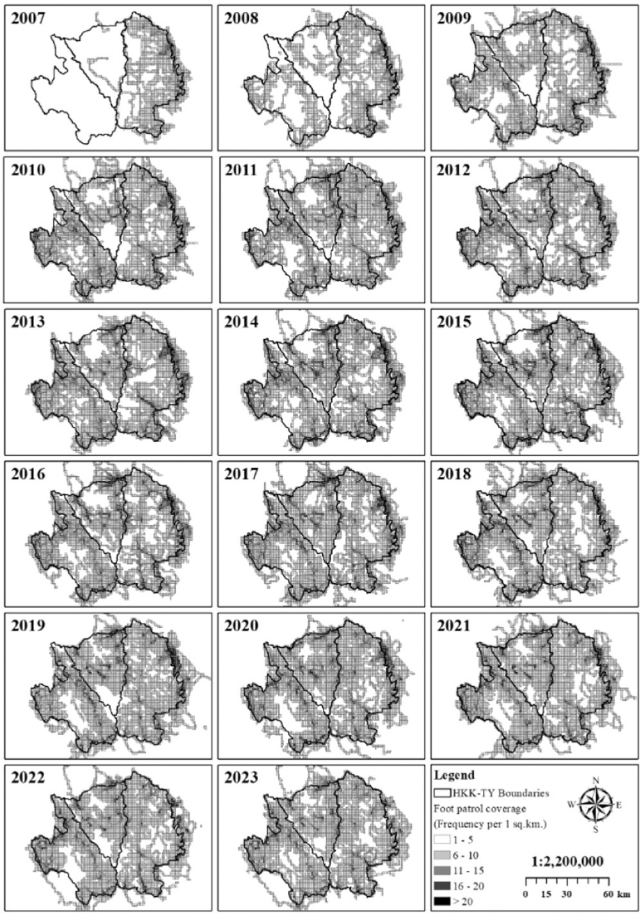

Fig. 4. Spatio-temporal coverage of the SMART foot-patrol carried out in Huai Kha Khaeng-Thung Yai (HKK-TY) study area during 2007–2023 period. Darker grey tones correspond to higher coverage frequencies, while lighter grey indicates lower frequency. Each grid cell corresponds to 1-km^2 area. (Source: (DNP, 2022b).

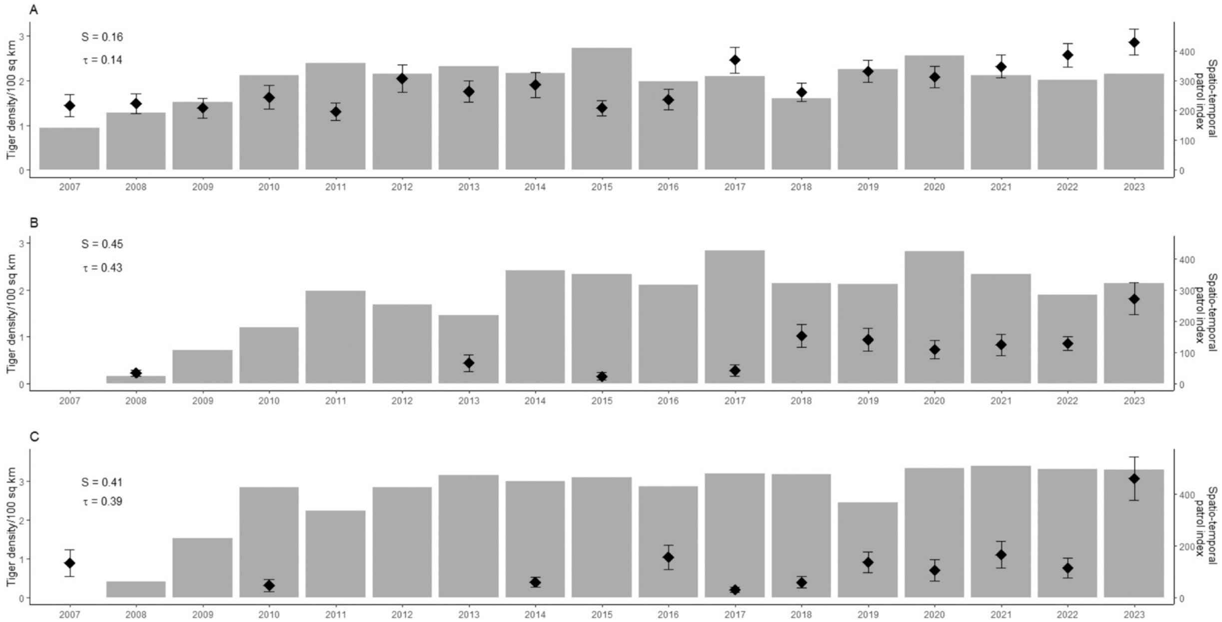

Fig. 5. Estimates of annual tiger population densities (per 100 km^2) with their corresponding measures of uncertainty and spatio-temporal index of patrol for Huai Kha Khaeng (A), Thung Yai East (B), and Thung Yai West (C). The inset values represent the standard deviation of the estimated total variance (S) and true temporal variance (τ) of annual tiger densities. Note that camera trap surveys to estimate tiger densities were carried out every year in HKK since 2004–05, in TYE since 2017 and in TYW since 2016, while SMART foot-patrolling was an annual feature since 2006 in HKK, 2007 in TYE, and 2008 in TYW. Camera trap surveys in TYE and TYW were infrequent in the initial years of the study due to resource constraints.

CRediT authorship contribution statement

Devcharan Jathanna: Writing – review & editing, Validation, Software, Methodology, Formal analysis. **Mayuree Sornsa:** Software, Resources, Formal analysis, Data curation. **K. Ullas Karanth:** Writing – original draft, Methodology, Funding acquisition, Conceptualization. **Somphot Duangchantrasiri:** Supervision, Resources, Project administration, Investigation, Data curation. **Chandan Kumar Pandey:** Validation, Software. **Pornkamol Jornburom:** Writing – review & editing, Resources. **Saksit Simcharoen:** Project administration, Methodology. **Anak Pattanavibool:** Writing – review & editing, Writing – original draft, Supervision, Resources, Funding acquisition. **N Samba Kumar:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation. **Supalerk Klanprasert:** Project administration. **Piyapong Suebsen:** Project administration. **Permsak Kanishthajata:** Project administration.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

The authors do not have permission to share data.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2024.e03016.

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