CONTRIBUTED PAPER

Tiger density, movements, and immigration outside of a tiger source site in Thailand

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Abstract
Landscape-scale strategies for conserving wild tigers emphasize the role of core breeding populations (source sites) to replenish surrounding areas which have lost tigers. In Southeast Asia, a few potential source sites remain, particularly Huai Kha Khaeng Wildlife Sanctuary, Thailand (HKK). We investigated tiger density in two reserves (Mae Wong, Khlong Lan: MWKL) adjacent to HKK where tigers and their prey were scarce due to historic poaching but current management offered effective protection. Camera trapping revealed 10 adult tigers (four males, six females), at least two of which had immigrated from HKK. Spatially explicit tiger density was 0.359 tigers/100 km², 5.6 times lower than HKK. The population was breeding, with six cubs observed. Tiger movements (measured by σ, the spatial scale parameter) were twice as extensive in MWKL as in HKK, indicative of prey scarcity in MWKL. The disparity in density between MWKL and HKK reveals that tiger recovery is a slow process when prey are scarce, even when recovery areas are apparently well-managed and connected to a source site. We review source-recovery dynamics of tigers in other sites in Asia and find that low prey impedes landscape-scale recoveries elsewhere as well.

KEYWORDS
camera trap survey, dispersal, immigration, population recovery, SECR

1 INTRODUCTION

The focus of tiger (Panthera tigris) conservation efforts has shifted from single reserves to large heterogeneous landscapes comprised of habitat patches of differing quality and levels of connectivity (Vasudev et al., 2017). Fewer than 4000 tigers remain in the wild, occupying just 7% of the species historical range (Sanderson et al., 2006; Walston et al., 2010). The recovery of wild tigers will require securing core-breeding populations of tigers, or source sites, while maintaining landscape-scale connectivity between source sites and surrounding recovery areas (Harihar et al., 2018; Walston et al., 2010; Wikramanayake et al., 2011). The movement of tigers across landscapes is a key mechanism for avoiding inbreeding, increasing reproductive success, and maintaining
fitness and genetic diversity (Gour et al., 2013; Waser et al., 1986). This strategy integrates the crucial short-term necessity of maintaining existing concentrations of breeding tigers, with a longer-term goal of increasing tiger distribution and numbers across larger surrounding landscapes from which they have been extirpated or driven to low numbers.

The status of wild tigers is particularly critical in Southeast Asia (Lynam, 2010). Tigers are already extinct from three countries in Southeast Asia: Vietnam, Cambodia, and Laos (O’Kelly et al., 2012; Rasphone et al., 2019; Walston et al., 2010). They are extirpated from most forest areas of Myanmar (Lynam et al., 2006), and they are declining rapidly in Malaysia (Rayan, 2019). A single protected area, Huai Kha Khaeng Wildlife Sanctuary (HKK) in western Thailand, holds the largest breeding population (>55 adults) and highest density (2.01/100 km²) of tigers in Southeast Asia (Duangchantrasiri et al., 2015). HKK also constitutes the core of Thailand’s Western Forest Complex and is embedded in a large forested landscape of 17 contiguous protected areas that cover 19,000 km². The surrounding protected areas have intact forest habitats but tend to support few tigers due to historical events including logging and commercial poaching (DNP, 2010). Over the past 10 years, however, tigers from HKK have been documented emigrating into some of these surrounding protected areas (Pattanavibool & Phoonjampa, 2017), confirming HKK as a source site for replenishing tigers in the wider landscape. The recovery of tigers in these surrounding protected areas is the key to increasing tiger numbers and distribution at a landscape scale, but (except for neighboring Thung Yai Naresuan Wildlife Sanctuary) the density of tigers in the protected areas surrounding HKK is not known, highlighting a crucial question: Are tigers recovering in these peripheral sites?

Here, we investigated the status of the tiger population in two national parks connected to the north part of HKK: Mae Wong and Khlong Lan. Since 2011, these parks have intensified wildlife management and protection efforts, including widespread and intensive patrolling by well-trained rangers and long-term financial assistance from the Thai government (Department of National Parks, Wildlife and Plant Conservation) and an international NGO (World Wide Fund for Nature Thailand). Our study was in 2016, 5 years after this intensified park management began. Our aims were to: (1) quantify the abundance, density, and movements of tigers in these parks, (2) assess how dissimilar these parameters were from HKK, and (3) assess the extent of immigration of tigers from HKK into these parks.

## 2 STUDY AREA

The study was conducted in Mae Wong National Park and Khlong Lan National Park (hereafter, MWKL), in the Dawna Mountain Range, western Thailand (99°4′30″ E to 99°22′13″ E and 15°39′52″N to 16°20′35″N). These adjacent parks cover 894 km² and 300 km², respectively (Figure 1). Elevation ranges from 150 to 1964 m above sea level. There is a dry season (November–May) and a wet season (May–October). Average annual rainfall is 1200 mm and mean temperature is 27°C (Meteorological Department of Thailand, 2017). The major habitat types are mixed deciduous forest, secondary forest with bamboo, and semi-evergreen forest.

Mae Wong National Park is adjacent to HKK, with a mountain ridge (elevation to 1500 m) forming the border between the protected areas. Khlong Lan National Park is contiguous with Mae Wong to the north. These three protected areas form a single connected forest area theoretically accessible to tigers and with no natural or anthropogenic barriers to tiger movements (Figure 1).

Both parks were subject historically to intensive commercial resource use. Logging occurred throughout the parks in the 1970s and 1980s and was accompanied by commercial wildlife poaching to supply markets in surrounding towns (Phumanee et al., 2020). Populations of tigers and ungulate prey species plummeted during this period (Pattanavibool & Phoonjampa, 2017) and the parks have depressed densities of tigers and ungulates (muntjacs Muntiacus muntjak and Muntiacus feae, wild pig Sus scrofa, sambar Rusa unicolor, and gaur Bos gaurus) to this day (Phumanee et al., 2020).

## 3 METHODS

We used camera traps to identify individual tigers and estimate tiger abundance and density in a capture-recapture framework (Karanth & Nichols, 2002). To guide camera placement, we covered the study area with 8 × 8 km grid cells (64 km²), slightly smaller than the average home range size of female tigers in nearby HKK (70 km²; Simcharoen, Savini, Gale, Simcharoen, et al., 2014). We placed 2–3 paired cameras within each cell. A total of 82 camera locations were deployed across the parks, with average spacing of 3.3 km between locations. The design reduced the probability of tigers going undetected, and the dense camera spacing relative to expected home range sizes maximized opportunities for capturing and recapturing tigers in the sample population.

At each camera trap location, a pair of passive infrared camera traps (Bushnell Trophy Cam Aggressor and Cuddeback C1 Flash) was placed opposite each other to
photograph both sides of passing tigers. Cameras were attached to trees 50 cm above ground and operated for 24-h with a 30-s interval between captures. Cameras were placed along ridges, trails, streams, and forest roads; these topographic features are commonly used by tigers and thus maximize encounter rates. Cameras were checked every 3 weeks. The minimum convex polygon around the outermost camera sites encompassed 1048 km².

Due to the large area sampled and limited staff, we divided the area into three blocks and sampled blocks sequentially in three phases, shifting the trap array after 3–4 months to the next block. Sampling was conducted from December 2015 to September 2016 and completed in 10 months. Sampling in each block slightly exceeded the 45–60 days recommended to meet the closure assumption in tiger studies (Karanth & Nichols, 2002). However, studies of low-density populations like ours require extended sampling to obtain sufficient data (captures and recaptures), and capture-recapture studies for long-lived animals such as tigers can safely extend the sampling period (Dupont et al., 2019; Harmsen et al., 2020). We carefully inspected the individual capture histories of our population for evidence that population closure was violated (e.g., individuals disappearing, as might occur due to death or emigration), and we also tested the closure assumption statistically (see below). We defined 5-day occasions for capture-recapture analysis (1-day occasions would have entailed excessive 0’s in the capture history). We identified individual tigers by their unique stripe patterns on the flanks and limbs (Karanth & Sunquist, 1995). We identified sex by noting presence of genitalia of males.

Tiger density was estimated using spatially explicit capture-recapture (SECR) in a full maximum-likelihood framework, using software DENSITY 5.0 (Efford et al., 2004). SECR estimates detection probability (g0), which is the probability of capturing an individual at its home range center, and sigma (σ), a spatial scale parameter which indexes animal movements and home range

**FIGURE 1** Map of Mae Wong and Khlong Lan National Parks, showing camera trap locations, and specifying locations where tigers were detected and not detected in 2016. Numbers of individual tigers detected at cameras is specified. Surrounding protected areas are named. NP, National Park; WS, Wildlife Sanctuary.
size (Efford et al., 2004). Sigma is derived from captures of individuals at different camera locations. We assumed a Poisson distribution of tiger home-range centers. We employed the “incomplete trap layout” in DENSITY, whereby traps in blocks not being sampled are denoted as “inactive” and contribute no information to the calculations. We estimated tiger abundance using the region.N function in R (secr v4.2.2; Efford, 2020).

We added a buffer around the camera trap sampling area equal to four times the root-pooled spatial variance (RPSV) of tigers. RPSV is a measure of dispersion of detections around trap locations (Efford et al., 2016). Adding a buffer ensures that animals with home-range centers outside the state space (or “area of integration”), if they exist, have a negligible chance of being included in the sample (Efford & Fewster, 2013). We then applied a habitat mask that excluded agricultural land which borders MWKL to the east (Figure 1). The RPSV for tigers was 7697 m. We thus added a 30,000 m buffer around the sampling area (rounded down from 7697 \times 4 = 30,788), and after excluding agriculture non-habitat to the east, the final state space was 5481 km².

Behavioral differences between sexes are a major source of heterogeneity in capture-recapture studies of felids and other carnivores and should be taken into account when estimating density (Goldberg et al., 2015; Sollmann et al., 2011). Male and female tigers exhibit major differences in home range size and movement patterns (Goodrich et al., 2010; Simcharoen, Savini, Gale, Simcharoen, et al., 2014); these innate biological differences warrant sex-specific estimation of parameters in a SECR analysis. We therefore calculated density, \( g_0 \), and \( \sigma \) for each sex separately, using a full-likelihood multi-session analysis in DENSITY, with sex affecting \( g_0 \) and \( \sigma \). Tiger sex was coded as a session variable using multi-session models (Royle et al., 2014). We summed sex-specific density estimates to calculate total tiger density.

SECR models assume that the encounter rate of individuals declines with distance from their home range centers (Efford, 2004). We compared the fit of two detection functions, half-normal and negative exponential, using Akaike’s Information Criterion. We did not consider the hazard-rate detection function as it assumes a threshold drop-off in encounter rate and can yield biased results where hard boundaries do not constrain the population of animals (Efford, 2019). MWKL is surrounded on three sides by contiguous forest (Figure 1), thus largely lacking any barrier to movements, so we regarded the hazard-rate function as biologically unrealistic.

We also conducted a conventional closed-population capture-recapture analysis implemented in software CAPTURE (Otis et al., 1978; Rexstad & Burnham, 1991). We used CAPTURE to test population closure, to assess the possibility of transience, and to generate a second abundance estimate. For CAPTURE, we created capture histories of tigers in a standard X-matrix format (Otis et al., 1978). We used a block trapping approach to create our capture history, in which the first five days of trapping in each block is combined to form sample occasion 1, the second 5-day period from each block combined to form occasion 2, and so on (Karanth & Nichols, 2002). This allows each tiger across the entire sample area to be exposed to trapping during each occasion. We compared eight models that assume different sources of variation in capture probability: no variation M0, individual variation Mh, behavioral variation in response to capture Mb, variation across time Mt, and combinations of these. We used the discriminant function scores in CAPTURE to identify the most appropriate model. MWKL is connected to a potential source of dispersing tigers (HKK) that might infuse our population with transient individuals which pass through the area but do not reside there. Such animals would exhibit a nonspatial form of heterogeneity manifested in sparse capture histories resembling a trap-shy response (Karanth & Nichols, 1998). Therefore, we were particularly interested in model Mb, which describes this type of capture history. We used the closure test of CAPTURE, which is based on the time between first and last capture of individuals, to assess population closure.

We assessed residency status of our tigers based on presence of cubs (age < 1 year) with a tigress, or observation of marking behavior in camera trap photos and videos. Marking behavior included scraping the ground and spraying scent on trees; this indicates a resident animal with a defined territory (Smith et al., 1989). We compared our tiger photos with the tiger photo database of HKK (S. Duangchantasiri, pers. comm.), in order to (a) assess immigration of tigers from HKK into our population in MWKL, and (b) ascertain if tigers in our sample were exclusive to MWKL or if their ranges included HKK. HKK has a comprehensive annual record of tigers since 2005. Although our data are from a single year, we compare it to the source site dataset at HKK, which encompasses a 10-year period before our study. We could thus discern if our tigers were born in HKK and immigrated into our site.

### Results

In 9709 trap nights, we photographed tigers 118 times at 31 camera locations (38% of camera locations; Figure 1). We identified 10 adult tigers, including four males and six females. Tigers were concentrated in the southern portion of the study area (Mae Wong), with up to four
individuals (one male and three females) captured at the same site (Figure 1). All tigers were recaptured at least once, with an average of 11 recaptures per female (range 2–21) and 12 recaptures per male (range 2–24). We also captured six cubs (two, three-cub litters) belonging to two adult female tigers (Figure 2). Cubs were not included in calculations of population abundance or density.

In the SECR density analysis, the negative exponential model (AIC 1146.247, Log likelihood = −567.123) fit the data better than the half-normal model (AIC 1154.972, Log likelihood = −571.247), with ΔAIC of 8.7 between these models. Estimated densities under the negative exponential model were 0.279/100 km² for female tigers and 0.08/100 km² for males (Table 1). Combined tiger density was 0.359 tigers/100 km² (SE 0.129). This is 5.6 times lower than in neighboring HKK (2.01/100 km²). Estimated abundance (realized N) under the secr model was 10.9 (SE 0.89), similar to the secr estimate. Capture probability (p-hat) per 5-day occasion was 0.338. All tigers except one male were captured early during sampling (within the first month) and recaptured multiple times throughout the sampling period; this suggests that the population was closed to emigration and deaths, and that transient tigers were not a significant portion of this population. Accordingly, population closure was supported by the test in CAPTURE (z = −0.576, p = 0.282), and model Mb was not supported in CAPTURE (discriminant score = 0.38).

Two tigers in the MWKL population, a male and a female, were immigrants from HKK. Both individuals were originally detected as cubs in HKK: the female in 2005, and the male in 2012 (S. Duangchantasiri, pers. comm.). The straight-line distances between these immigrants’ natal ranges (site of earliest photos as cubs in HKK) and their adult ranges in MWKL (location furthest inside MWKL) were 30 km for the female and 55 km for the male. We observed indicators of residency (presence of cubs; marking behavior) for four of six females and two of four males, including both of the immigrants from HKK (Figure 2). Although HKK provided two immigrants, none of the MWKL tigers matched any tiger currently known in

![Figure 2](image)

**FIGURE 2** Adult female tiger (“F3”) with cub in Mae Wong National Park, Thailand, 2016. Other photos and videos revealed two further cubs in this litter (litter of 3). This female was born in 2005 in Huay Kha Khaeng Wildlife Sanctuary—The adjacent tiger source site. Although the tiger population in Mae Wong-Khlong Lan is small, it is connected to a source site supplying occasional immigrants, such as F3, that become breeding residents.
HKK. Thus, MWKL tigers were not merely peripheral individuals of the HKK population whose ranges extended into a different administrative unit.

Accurate estimation of the SECR scale parameter ($\sigma$) depends on animals having stationary activity centers during a study (Royle et al., 2016). Based on maps of captures and recaptures of each tiger in our population, we found no indication that activity centers shifted over the study. This accords with the composition of our population, which was predominantly resident animals. Resident tigers tend to have stable home ranges where an individual resides for multiple years (Smith, 1993), far longer than the duration of our study. Thus, our estimates of tiger movements should be robust to the potential issue of shifting activity centers.

### 5 | DISCUSSION

We provide the first status assessment of a recovering tiger population connected to the most important tiger source site in Southeast Asia (Huai Kha Khaeng). Our study reveals the disparity in tiger density and movements between a source site and an adjacent recovery site. Our sex-specific analysis revealed substantial differences between male and female tigers in detection probability ($g_0$) and especially scale of movement ($\sigma$). Both $g_0$ and $\sigma$ were larger in males than females, as found in studies of other large felids (Sollmann et al., 2011; Tobler et al., 2013); these sex differences are an important source of variation that should be accounted for when estimating density (Efford & Mowat, 2014).

Tiger density was low in MWKL, with just 0.359 individuals/100 km$^2$. Tiger densities well below 2/100 km$^2$ are common in Southeast Asia, due to over-hunting of prey animals, direct poaching of tigers, widespread conversion of productive lowland forest to agriculture, and inherently low carrying capacity of remaining upland forests. For example, tiger density (per 100 km$^2$) in 13 other sites in Southeast Asia with SECR estimates is: 0.81 in Htamanthi, Myanmar (Naing et al., 2019); 0.63 in Thap Lan, Thailand (Ash et al., 2020); 0.61 in Temenggor, Malaysia (Rayan & Linkie, 2015); 0.34–0.87 at five sites in Sumatra (Sunarto et al., 2013); 0.74–1.94 at three sites in Sumatra (Luskin et al., 2017); 0.36 in Kuiburi, Thailand (Steinmetz et al., 2012); and 0.34 in Pangsida, Thailand (WWF Thailand et al., 2014).

At least 20% of the tigers we observed in MWKL were immigrants from HKK, including one of the resident female breeders (Figure 2), and a resident male. Connectivity between tiger populations can provide multiple benefits, including recolonization of empty habitat, demographic rescue, population augmentation, and inbreeding avoidance (Vasudev et al., 2017). MWKL may have received most of these benefits from HKK to some degree. But despite the proximity of HKK and its contribution of immigrant tigers, tiger density in MWKL remains nearly six times lower than in HKK.

Why is tiger density in MWKL so low compared to HKK? There is no evidence that tigers are poached in MWKL. The main difference between these sites is that prey abundance is much lower in MWKL. Numerous studies have shown that the distribution and density of tigers in an area is largely a function of the availability of large ungulate prey such as gaur, sambar, and banteng (Karanth & Sunquist, 1995; Simcharoen et al., 2018; Simcharoen, Savini, Gale, Roche, et al., 2014). Notably, in MWKL these key prey species are severely reduced or extirpated compared to HKK. For example, banteng (*Bos javanicus*), which are the most-consumed prey species by tiger in nearby HKK (Simcharoen et al., 2018) were

### TABLE 1

The following table provides parameter estimates from spatially explicit capture–recapture (SECR) models for male and female tigers in Mae Wong-Khlong Lan National Parks, Thailand, 2016.

| Sex     | Parameter                  | Detection function | Half normal | Negative exponential |
|---------|----------------------------|--------------------|-------------|----------------------|
| Male    | Density (SE)               | 0.084 (0.046)      | 0.080 (0.043) |
| 95% CIs of density | 0.031–0.23 | 0.030–0.217 |
| g0 (SE) | 0.065 (0.03)               | 0.361 (0.334)      |
| $\sigma$ (SE) | 13,522 m (2049 m) | 7255 m (1487 m) |
| Female  | Density (SE)               | 0.263 (0.114)      | 0.279 (0.121) |
| 95% CIs of density | 0.116–0.593 | 0.124–0.63 |
| g0 (SE) | 0.074 (0.012)              | 0.173 (0.04)       |
| $\sigma$ (SE) | 5509 m (560 m) | 3009 m (376 m) |

Note: Estimates from two different detection functions are compared. Density is per 100 km$^2$. Capture probability ($g_0$), and scale of movement ($\sigma$) are given. 

Abbreviations: CI, confidence interval; SE, standard error.
extirpated in MWKL due to commercial poaching decades ago (Phumanee et al., 2020). Gaur and sambar still occur in MWKL but occupy just 22% and 24% of the area (Phumanee et al., 2020); in contrast, occupancy rates for these species are over three times higher in HKK (Duangchantrasiri et al., 2019). This low prey abundance is a legacy of commercially driven poaching which accompanied extensive logging concessions in the past (Phumanee et al., 2020). It is likely that the scarcity of these large ungulates is a significant constraint on current tiger distribution and abundance in MWKL. Indeed, MWKL tigers were concentrated in the western half of Mae Wong National Park and were mostly absent elsewhere (Figure 1)—this distribution corresponds strongly with the distribution sambar and gaur (Figure 3).

The effect of a sparse prey base is further revealed in tiger movements. Home range size of female tigers declines with increasing prey density (Simcharoen, Savini, Gale, Simcharoen, et al., 2014). That is, females in areas with abundant ungulates tend to have small home ranges because they do not need to move extensively to find food. Male home ranges are tied more to dispersion of females than to prey directly (Karanth & Nichols, 2017), but space use by males should adjust similarly to prey density through its dependence on female density. Although home range sizes of tigers in MWKL are unknown, the movement parameter ($\sigma$) estimated in SECR is a signal of home range size (Royle et al., 2014). By comparing our estimate of $\sigma$ with the same parameter for tigers in HKK, we can infer home range size differences between the two sites. To enable comparison, we ran a model with sexes combined, under a half-normal detection function, similar to Duangchantrasiri et al. (2015) in HKK. Movement of tigers in MWKL under this model was 7433 m, which is over twice higher than movements of tigers in HKK ($\sigma = 3495$ m; Duangchantrasiri et al., 2015). This difference indicates substantially larger home ranges and more extensive movements in MWKL, as would be expected if prey were scarce.

The large-scale movements and extensive space use of resident tigers in MWKL points to low prey abundance as the driver of low tiger density, probably by (a) suppressing reproduction by resident females within MWKL and (b) constraining the capacity of MWKL to accommodate immigrants. Degraded habitats (i.e., low prey) often limit the potential contribution of immigration in apex predator recoveries, by constraining

**FIGURE 3** Map of Mae Wong and Khlong Lan National Parks, Thailand, showing camera trap locations with and without detections of gaur and sambar (2016)
successful colonization and recruitment into the population (Stier et al., 2016). Continued monitoring of density and movements will allow the parks to assess if management interventions are working for tigers.

5.1 Source-recovery dynamics of tigers in Asia

The comparative status of tigers in low-density recovery sites, and in nearby source sites with a higher density, has been documented in a few other places. In northeast China, tigers were extirpated decades ago due to poaching, but began recolonizing in the late 1990s from adjacent source populations in Russia (Wang et al., 2018). As of 2014, a small breeding population of about 20 tigers occurs in northeast China, though density is still very low, 0.2–0.27 tigers/100 km² (Wang et al., 2018). Tiger abundance on the Russian side appears to also be low (Wang et al., 2015), but the population is linked (within Russia) through dispersal to a much larger Russian source population (in Sikhote-Alin Reserve), where the density is nearly 1/100 km² (Miquelle et al., 2015; Sorokin et al., 2016). Thus, tiger density in the Chinese recovery site remains 3.7 times lower than in the source site, despite extensive habitat on the Chinese side and over 10 years of intensive management (snare removal, food supplementation, prey augmentation, patrolling and outreach, and monitoring). A major constraint to recovery in China is low abundance of the tigers’ main prey, sika deer (Wang et al., 2018); this resembles the situation at MWKL.

A second example shows that more rapid and substantial recoveries are also possible. In 2009, Parsa Wildlife Reserve in Nepal supported a relatively low density of tigers (0.61/100 km²) due to low prey abundance and occasional tiger poaching (Lamichhane et al., 2017). Parsa is adjacent to Chitwan National Park, which supported a large, stable population of 3.8–4.5 tigers/100 km² (Dhakal et al., 2014; Karki et al., 2015). In 2010, Parsa initiated habitat improvements and other interventions which led to a five-fold increase in ungulate prey. As a result, immigrants from Chitwan began to settle in Parsa, and tiger density steadily increased to 0.78 in 2013 and 1.38 in 2016 (Lamichhane et al., 2017). Thus, density in this recovery site, which was initially 7.4 times lower than the source population in Chitwan, rose over 7 years to a level 3.3 times lower than Chitwan.

5.2 Implications for tiger recovery

Sufficient forested habitat exists to support a range-wide doubling of wild tigers in Asia (Joshi et al., 2016), but this potential is negated by low prey abundance in much of it (Di Marco et al., 2014). A recent range-wide analysis of tiger recovery sites in Asia identified MWKL as potentially supporting 20 resident tigers if prey abundance was similar to HKK (Harilhar et al., 2018). Currently MWKL is halfway to this target. The disparity in tiger density between MWKL and HKK, despite 5 years of strong protection preceding our study, no evidence of tiger poaching, and unimpeded connectivity to a source population, reveals that tiger recovery at landscape scales in Southeast Asia is a slow process. Raising tiger density in MWKL to a level matching the source site (i.e., >2 tigers/100 km²) will require maintaining effective ranger patrolling and community outreach that limits poaching of tiger prey, as well as more direct interventions to increase prey, such as improving habitats for ungulates (by creating grasslands and saltlicks) and augmenting the sparse populations of sambar using captive animals.

Our results have practical and policy implications for range-wide conservation efforts of tigers. First, recovery efforts at large spatial scales may take decades to achieve, even where connectivity is high. Second, prey augmentation might be needed to accelerate tiger recovery outside of source sites. Third, tiger range countries must make long-term policy commitments that maintain forest cover and connectivity between source sites and surrounding landscapes. These considerations are relevant to recovery efforts for apex predators in general, highlighting the importance of multi-scale management strategies that raise carrying capacity in peripheral recovery areas (by increasing prey abundance) so that predators immigrating from connected source sites can recruit into the population.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.
AUTHOR CONTRIBUTIONS
Worrapan Phumanee: Conceptualization; methodology; formal analysis; investigation; data curation; and writing-original draft. Robert Steinmetz: Conceptualization; methodology; formal analysis; investigation; data curation; and writing-original draft, review and editing.
Rungnapa Phoonjampa: Conceptualization; writing-review and editing; investigation; funding acquisition; and project administration. Suthon Weingdow: Coordinated data collection. Surachai Phokamanee: Coordinated data collection. Naris Bhumpakphan: Conceptualization. Tommaso Savini: Conceptualization; writing-review and editing; and funding acquisition.

DATA AVAILABILITY STATEMENT
The data used in this study are available upon discussion with the authors.

ETHICS STATEMENT
Research followed protocols approved by the Department of National Parks, Wildlife and Plant Conservation. The study was observational, and involved no human or animal subjects.

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