



Original research article

Protected areas sustain Amur tiger populations in the Russian Far East's multiple-use landscapes

Scott J. Waller^{a,*}, Aleksandr N. Rybin^b, Ekaterina I. Nikolaeva^b, Anton V. Semyonov^b, Svetlana V. Soutyrina^c, Jonathan C. Slaght^a, Ivan V. Seryodkin^d, Dale G. Miquelle^a

^a Wildlife Conservation Society, New York, USA

^b ANO WCS, Vladivostok, Russia

^c Sikhote-Alin Biosphere Reserve, Terney, Russia

^d Pacific Institute of Geography, Far Eastern Branch of the Russian Academy of Sciences, Vladivostok, Russia

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ABSTRACT

Protected areas are a hallmark of conservation, yet their ability to support endangered species can be compromised by human use in adjacent lands. In the Russian Far East, a network of protected areas has been established to conserve biodiversity, including the endangered Amur tiger (*Panthera tigris altaica*). However, human disturbance in/around protected areas may jeopardize tiger populations. In this study, we surveyed 504 camera trap sites over 4 years (2018–19–2021–22) in an 8322 km² multiple-use landscape in the Central Sikhote-Alin Mountains to estimate tiger density and survival in relation to human development and use, including previously undocumented forest roads. We estimated a stable, low population density of 0.27 tigers (95 % CI [0.18–0.31]) per 100 km² in places further from main roads and in high-quality habitat. Female tigers captured predominantly in protected areas had higher survival ($\varphi = 0.90$ [0.60–0.98]) than those in multiple-use areas ($\varphi = 0.51$ [0.30–0.72]). The number of females detected with cubs was also twice as high in protected areas. Analyzing high-resolution satellite imagery, we traced 7828 km of roads. In places with intense logging traffic, the odds of detecting individual tigers more than one year decreased by 92 %. While protected areas ensured higher annual survival of female tigers, greater cub production, and a stable population, logging operations in multiple-use lands represented a key threat, probably by increasing chances of poaching. Overall, our study area remains far from tiger recovery goals, and we urge more investments in law enforcement, especially outside of protected areas.

1. Introduction

Conservation practitioners aim to understand the most pressing threats to endangered species and prioritize responses under constraints on time, funds, and resources. This becomes especially challenging in multiple-use landscapes where human disturbance and varying human tolerances for wildlife require diverse approaches to conservation. The establishment of protected areas has been a hallmark approach by the international community to set aside lands for endangered species and biodiversity broadly (IUCN, 2016;

* Correspondence to: 2300 Southern Blvd, Bronx, NY 10460, USA.

E-mail address: swaller@wcs.org (S.J. Waller).

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UNEP, 1992). But it is often unclear whether there are positive spillover effects into adjacent multiple-use lands, or the opposite: negative effects from adjacent lands on protected areas, such as human use in surrounding lands that result in human-wildlife conflicts (Geldmann et al., 2013; Terraube et al., 2020; Watson et al., 2013; Woodroffe and Ginsberg, 1998).

In Asia, the tiger (*Panthera tigris*) has undergone severe population declines over the last 150 years, with 3726–5578 remaining individuals estimated today (Goodrich et al., 2022) occupying only 5–10 % of the species' former range (Sanderson et al., 2025). Poaching, habitat loss and fragmentation, and prey depletion continue to threaten tigers and have caused their recent extirpation from Vietnam, Cambodia, and Laos PDR in just the last 25 years (Johnson et al., 2016; O'Kelly et al., 2012; Rasphone et al., 2019). In 2010, Walston et al. proposed that the key to the conservation of tigers is the creation and protection of "source sites", so named because they represent core, well-protected areas from which secure, reproducing populations can generate offspring that expand into larger tiger conservation landscapes. The authors defined source sites as areas with the potential to maintain 25 breeding females, embedded in a larger landscape with the potential to contain at least 50 breeding females, and which had a legal mandate for protection. Several governments and major NGOs have invested heavily in securing source sites in multiple countries across Asia. There have been some key successes such as in Thailand's Western Forest Complex (Duangchantrasiri et al., 2024) and Russia's Land of the Leopard National Park (Hötte et al., 2016; Matiukhina, 2020), as well as failures such as in Laos PDR's Nam Et-Phou Louey National Protected Area (Johnson et al., 2016). There remains some debate over whether this source site approach is an effective conservation strategy for tigers.

Wikramanayake et al. (2011) highlighted the lack of focus on connectivity to maintain genetic diversity, without which the source sites expounded by Walston et al. (2010) would likely eventually succumb to disease, low ability to adapt to environmental change, and inbreeding depression. Indeed, isolation has proven a challenge for small populations in India (Gopal et al., 2010) and recently recovered Amur tigers in southwest Primorye, Russia, which are isolated from the larger population in the Sikhote-Alin Mountains (Jeong et al., 2024). Accelerating human development outside of protected areas threatens further isolating tiger populations at source sites (Carter et al., 2020; Schoen et al., 2022). Increasing focus is therefore being placed on increasing human-tiger coexistence (Tiger Conservation Coalition, 2021), as well as conserving key movement corridors (e.g., Asia's Linear Infrastructure Safeguarding Nature (ALIGN) project; Habib and Saxena, 2024) to connect tiger populations across multiple protected areas.

In Northeast Asia, Amur tigers (*P. t. altaica*; Fig. 1) live in what are probably the most extreme environments encountered by any tiger subspecies. Due to long, cold winters and deep snows, prey densities are the lowest recorded in any part of the tiger's range (Miquelle et al., 2010). Consequently, home ranges are the largest reported for the species (Goodrich et al., 2010; Hernandez-Blanco et al., 2015; Klevtcova et al., 2021). Even though an extensive network of protected areas has been created in the Russian Far East to support tiger conservation (Darman et al., 2018), no single protected area (or network of contiguous protected areas) is large enough to protect a source site of 25 breeding female tigers (Carroll and Miquelle, 2006; Walston et al., 2010). Only 20 % of tiger habitat lies within federal protected areas; the remaining lands are managed as hunting and logging concessions, mostly on federal forest lands, with a growing network of forest roads. These are built primarily by logging companies to access concessions, but they also allow other forms of human use (Smirnov et al., 2013). The construction of these roads is concerning because they may directly fragment wildlife habitats (Forman et al., 2003; Haddad et al., 2015; Olson and van der Ree, 2015), disrupt animal movement (Northrup et al., 2012; Prokopenko et al., 2017; Scraftford et al., 2018), and cause noise and light pollution that can alter behaviors and reduce fitness (Newport et al., 2014; Shannon et al., 2016). Roads also cause wildlife mortality by collisions with vehicles (Driessen, 2021; Loss et al., 2014; Oleynikov et al., 2025) and can lead to increased poaching levels due to easier access to wildlife (Benítez-López et al., 2017; Ripple et al., 2016; Slaght et al., 2019; Smirnov et al., 2013). As the number of roads in this region increases (Bergen et al., 2020; Smirnov et al., 2013), there is an urgent need to understand how human disturbance is impacting Amur tiger population demographics in the multi-use landscapes of the Russian Far East, and to what degree protected areas are supporting the recovery and persistence of these populations.



Fig. 1. An Amur tiger photographed by one of our camera traps in the Central Sikhote-Alin Mountains, Russian Far East. Image © ANO WCS | Udege Legend National Park.

To better understand tiger population dynamics across a multiple-use landscape and the efficacy of protected areas in supporting Amur tiger survival and reproduction, we established an extensive camera trap monitoring program in the central Sikhote-Alin Mountains of the Russian Far East. As a major form of human disturbance in the region, we collected data on the current extent of roads in our study area and used generalized linear models to understand observed patterns of vehicle traffic over 4 years (2018–19–2021–22). Using spatial capture-recapture (SCR) models (Borchers and Efford, 2008; Efford and Schofield, 2020), we analyzed the effects of protected areas and roads on Amur tiger population density and tested whether tiger survival and recruitment was influenced by the proportion of image captures in protected areas. Finally, we used logistic regression to investigate whether individual tiger tenure on the landscape was negatively affected by different types of human use on forest roads.

2. Methods

2.1. Study area

The central Sikhote-Alin Mountains of the Russian Far East are situated along the coast of the Sea of Japan, with the region largely divided by the low-elevation Sikhote-Alin ridge (most peaks below 1000 m) running parallel to the coast. On the eastern slope of the mountains, average temperatures range from highs of 23°C in August to lows of −16°C in January. On the western slope, average temperatures range more widely from 29°C in July to −26°C in January. The region is heavily forested with a monsoonal climate (average annual rainfall in Terney: 843 mm) and heavy summer rains driving high productivity. Human settlements are small and dispersed among protected areas and vast areas leased for hunting and logging. Human population density is low with 0.49 and 0.90 people/km² in the Terneysky and Krasnoarmeysky Districts, respectively, which include most of our study area. The region includes a mixture of broadleaf temperate and boreal forests. Amur tigers primarily prey on four ungulate species: wild boar (*Sus scrofa*), red deer (*Cervus canadensis xanthopygus*), roe deer (*Capreolus pygargus*), and sika deer (*Cervus nippon*) (Kerley et al., 2015; Miquelle et al., 2010). These species depend on mast-producing Mongolian oak (*Quercus mongolica*), predominantly on the eastern slope, and Korean pine

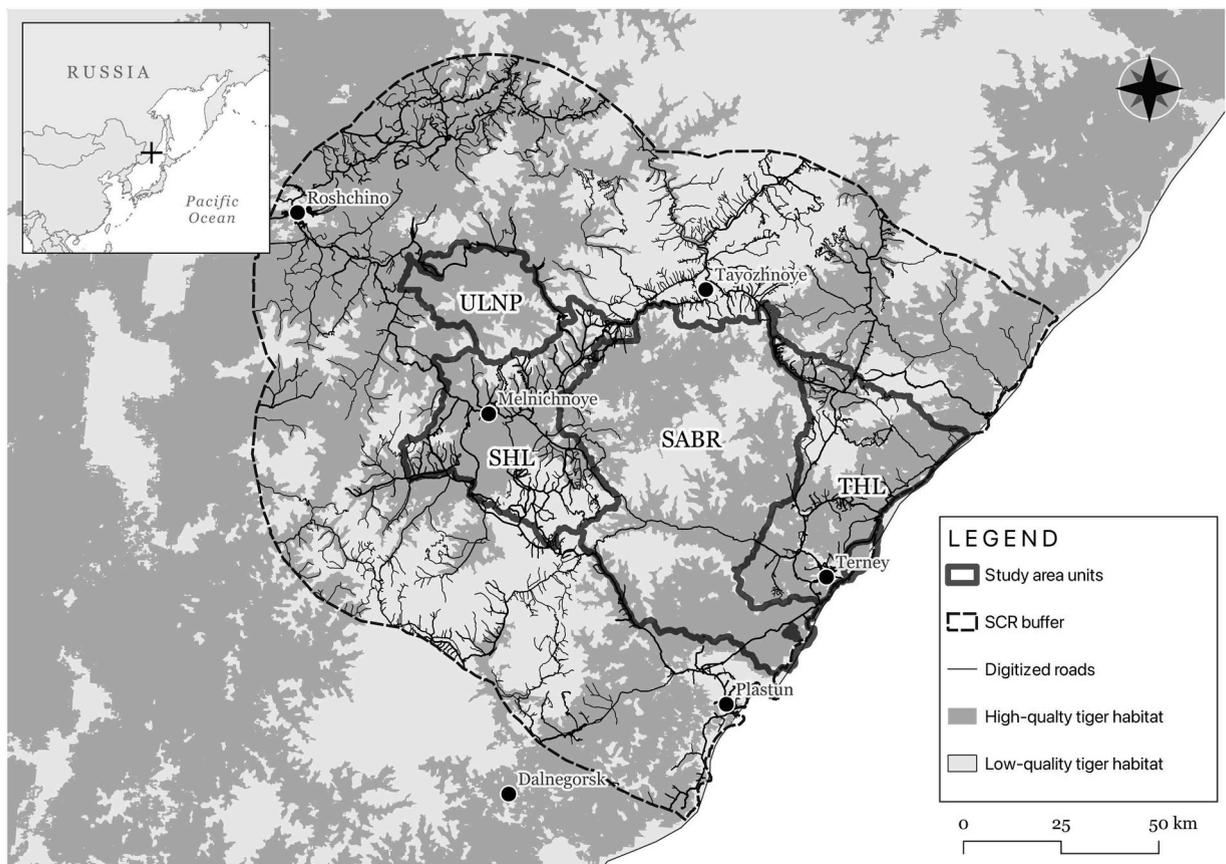


Fig. 2. Map of study area in Central Sikhote-Alin Mountains, Russian Far East. Tiger habitat is presented as high or low quality as identified by Hebblewhite et al. (2014). Our camera trapping took place within four study area units based on management type (west to east): Udege Legend National Park (“ULNP”); Sidatun Hunting Lease (“SHL”); Sikhote-Alin Biosphere Reserve (“SABR”); and Terney Hunting Lease (“THL”). Roads were digitized within a 25,000 km² region, defined by a 24 km buffer around our study area for spatial capture-recapture (SCR) analysis. Main settlements are labeled.

(*Pinus koraiensis*) further inland (Bromley and Kucherenko, 1983).

Our study was specifically conducted in the 8322 km² congruous territory of Sikhote-Alin Biosphere Reserve (4016 km²), Udege Legend National Park (766 km²), Terney Hunting Lease (1778 km²), and Sidatun Hunting Lease (1762 km²; Fig. 2). This study area and specific sampling locations were selected to intentionally include both protected areas and multiple-use landscapes to better understand the influence of anthropogenic factors and the relative importance of protection in influencing tiger population dynamics. Both hunting and selective logging are allowed on the hunting leases, while the two protected areas prohibit these activities within their borders. Logging is an important industry for the region's economy, and the number of roads in the region has been increasing to support timber extraction (Bergen et al., 2020).

2.2. Camera trap deployments

We placed 1 pair of camera traps in cells of a 7 × 7-km grid across our study area in four consecutive fall/winters (2018–2019–2021–2022). Assuming an average female home range of 400 km² (Goodrich et al., 2010), this grid size allowed sufficient opportunity for individual tigers to be captured at multiple cameras to estimate SCR detection parameters. Camera sites in each grid cell were selected to maximize detections of tigers along forest roads, trails, and ridges. Cameras were placed roughly 4 m away and on either side of the linear feature (no more than 100 m apart) to photograph both sides of passing tigers for later individual identification. Cameras were deployed each year in September–October and retrieved in December–January. This provided a 90-day sampling period when cameras were active to meet the assumption of temporal closure in our SCR analyses (Soutyrina et al., 2013).

2.3. Extent of roads and modeling human use

The construction of forest roads and their use by humans are major types of human disturbance in our study area. Yet, a detailed assessment of their extent is lacking. We therefore visually examined satellite imagery across our study area and manually traced any roads we found. We collaborated with the University of Montana and Panthera to use the most up-to-date imagery available from the ESRI, Bing, Yandex, and Google Earth Satellite plug-ins available in QGIS, which typically ranged in date from 2017 to 2023. We differentiated between forest roads (primarily built for logging and mostly unmaintained) and rivers (which often looked similar on satellite images) based on their connectivity to larger roads, the presence of logging landings, and adjacent skidder tracks. Main roads (e.g., residential roads within settlements, or improved roads connecting settlements) were copied from the OpenStreetMap database (Ramm et al., 2010) and visually inspected for accuracy. We were limited by the quality of satellite imagery available and could not accurately capture the construction of new roads built during our four study years that might have resulted in annual differences in road density. However, the construction of new roads during this period was likely minimal relative to the number of roads already present. We therefore believe our results mostly capture the true extent of roads in our study area. We compared summary statistics with those from roads provided by the Global Roads Inventory Project (GRIP; Meijer et al., 2018), which was used by Carter et al. (2020) to assess the risk of roads to tigers across the species' range.

The cameras we deployed on forest roads and trails to detect tigers also captured images of human use. We categorized images of vehicle traffic as: recreational/private vehicles, vehicles clearly associated with logging (including trucks hauling logs, equipment trucks hauling skidders and tractors, and vehicles carrying supplemental equipment like living quarters), and vehicles engaged in spotlight poaching. Spotlight poachers use powerful lights to find and shoot wildlife at night and were thus easily identified based on the strong beams of light coming from passing vehicles, usually with a person holding a rifle as well. After categorizing images, we calculated relative abundance indices (RAIs) of each traffic type at each camera site, k , by:

$$RAI_k = \frac{y_k}{t_k} \times 100,$$

where y_k is the average number of independent detections and t_k is the average number of days operational for the two cameras active at site k . Cameras at the same site typically had similar numbers of detections and days operational. If they did differ, we considered the average RAI_k as a reasonable summary of the variation in traffic that occurred on these roads. We considered detections of traffic to be independent if vehicles were clearly distinguishable, or, when they were not distinguishable, when they were at least 30 min apart (Sollmann, 2018).

We used negative binomial generalized linear models (GLMs) with a log link to test whether different types of vehicle traffic could be predicted by 5 covariates: (1) Euclidean distance to settlements; (2) Euclidean distance to main roads; (3) terrain ruggedness; (4) camera site in protected area or hunting lease; and (5) year. Continuous covariates were centered to mean 0 and scaled to a standard deviation of 1. We used the "MuMIn" package in R (Bartoń, 2022) to implement a stepwise regression process and identify the top model by Akaike's Information Criterion adjusted for small sample size (AICc; Burnham and Anderson, 2002). We then used the "DHARMA" package in R (Hartig and Lohse, 2022) to evaluate model fit by evaluating normality of residuals with Komolgorov-Smirnov tests and any dispersion issues through DHARMA nonparametric dispersion tests.

2.4. Tiger population density

We used SCR models to evaluate whether Amur tiger density differed between protected areas and hunting leases where logging, hunting, and recreational human use were permitted. Spatial Capture-Recapture models separate the observation process of detecting

animals (here, tigers at camera traps) from the latent process of population density. The detection parameters of g_0 (detection probability at an individual tiger's activity center) and σ (scale parameter describing the decline in detection probability with distance from activity center) and the population density parameter, D , can be estimated by maximizing the full likelihood, modeling the parameters in a joint distribution of the number of animals identified and each animal's detection history conditional on it being identified (Borchers and Efford, 2008). These models allow density to be modeled in response to spatial and temporal covariates.

Before we tested covariate effects on tiger density, we used AICc to identify the best-supported detection model, testing between hazard and halfnormal detection functions as well as effects of sex and/or time. Then, we developed 13 candidate models for tiger density as explained by single covariates related to: 1) high or low-quality tiger habitat, defined by Hebblewhite et al. (2014); 2) road density, summarized using a 11 km-radius moving window based on the average size of a female tiger's home range then z-transformed; 3) road buffer effects at 0.5, 1, and 3 km; 4) land management type (protected area or hunting lease); and 5) both categorical and linear effects of year. Road covariates were summarized based on all digitized roads as well as main roads only. For univariate models with evidence of meaningful covariate effects (standardized coefficients > 0.5), we tested additional models that included additive and interactive effects between uncorrelated covariates. These models allowed us to investigate spatial relationships between tiger density and different spatial scales of roads and to contextualize them with other potentially important covariates. We selected the top model with the lowest AICc value and applied a likelihood-ratio test to determine if the additional covariates in the density model significantly improved upon the null model of constant density. All SCR analyses and likelihood ratio tests were done using the "secr" package in R (Efford, 2025).

2.5. Tiger survival, recruitment, and movement

To estimate Amur tiger survival, recruitment, and movement rates, we used likelihood-based open SCR models (Efford and Schofield, 2020; Ergon and Gardner, 2014). Initial data exploration found many individuals detected in only one year and at the edge of our study area – a common occurrence for study areas without natural borders – meaning non-spatial models were likely to confound survival with emigration or even smaller shifts in activity centers. We therefore used spatial forms of Jolly-Seber-Schwarz-Arnason (JSSA) models (Pledger et al., 2010) provided in the "openCR" package version 2.2 (Efford, 2023) to explicitly model movement of tiger activity centers between sampling years. Though open SCR models include an estimate of density, datasets with low sample sizes can have issues with computational time and convergence of parameter estimates (Efford, 2023). We already estimated density with closed SCR models, and because of our low sample size, we used the conditional likelihood formulation (i.e., we estimated the remaining parameters by maximizing the likelihood of parameter values conditional on the number of individuals observed) to reduce the computational demand and accelerate the estimation process.

We stratified our data by sex to estimate survival, recruitment, and movement of activity centers of male and female Amur tigers separately. We used a stepwise approach to find the most-supported JSSA model: first, we compared AICc between hazard half-normal and hazard exponential detection functions and tested for variation in year. Next, we selected the model with the lowest AICc among five movement kernel types (bivariate t , exponential, and gamma kernels, as well as independent and static movement). We tested whether allowing year-specific estimates of survival, recruitment, and the movement kernel scale parameter(s) provided better support according to AICc. Lastly, we investigated whether protected areas provided refuge for Amur tiger survival and reproduction by testing whether tigers predominantly detected in protected areas (defined as >50 % of detections across all years) differed in survival, recruitment, and movement compared to those predominantly detected outside. We fit a final model with both sexes combined for an average across sex and thus total population estimate of adult Amur tiger survival, recruitment, and movement.

To infer differences in cub production, we compared the ratio of the number of females detected with cubs to those without, with the two groups of tigers divided by whether detections predominantly occurred in protected areas or hunting leases. We used a Pearson's chi-square test of homogeneity to test for significant differences ($\alpha = 0.05$) between these two groups. We acknowledge that cub detection at camera traps was probably low. Their small body sizes make them less likely to be detected by infrared sensors, and they may stray from the road or trail. Female tigers with cubs are also known to avoid roads and trails used by male tigers (Yudakov and Nikolaev, 2012), further reducing their probability of detection. Still, these challenges were likely the same between protected areas and hunting leases, so we consider observed ratios to still be informative about possible differences in cub production.

2.6. Relationship between human use and tiger persistence

Human use of roads is variable in space and time, which means individual tigers' exposure to this use is similarly variable. This also makes evaluating this variable incompatible with open capture-recapture models of survival that require year-specific covariate estimates for individual animals even in years when they were not detected. We therefore took a simplified approach and used logistic regression to determine whether the *persistence* of tigers was related to their *exposure* to different types of vehicle traffic. We defined *persistence* as the probability that a tiger first captured in the first two years of sampling would be detected in at least one subsequent year. We did not include tigers first captured in the third year of sampling because of the increased uncertainty whether missed captures of these individuals in the fourth, last year was due to imperfect detection or actual mortality / emigration. We estimated the *exposure* of each tiger, i , to variables of human use as a weighted average,

$$Exposure_i = \frac{\sum_k^c (RAI_k \times n_k)}{N},$$

where k is an individual camera site, C includes all cameras k where tiger i was detected, n_k is the number of captures of tiger i at site k , N is the total number of detections of tiger i at cameras C , and RAI_k (Equation 1) is the relative abundance of the variable of interest at site k . Assuming that tigers spent more time in places where they were captured more often, this equation provided an index of each tiger's exposure to the traffic type of interest. This framework allowed us to determine if the *exposure* of tigers to higher vehicle traffic decreased the probability of observing them in later years (i.e., their *persistence*). We acknowledge that this method confounds recapture probability with actual survival but believe this was the best way to make use of our data and investigate potential impacts of these time-varying covariates on tigers. As in our analysis of human use above, traffic covariates were centered and scaled before analysis.

3. Results

3.1. Data collection

Over four years (2018–19–2021–2022), we obtained data from cameras at 504 sites across our study area in Central Sikhote-Alin that together monitored 40,751 trap nights (Table 1). A small number of additional cameras were stolen each year or did not function properly. Within our 90-day sampling periods, we documented 1206 independent captures of 69 unique adult Amur tigers (Table 1).

3.2. Extent of roads and modeling human use

We digitized a total of 7828 km roads within our study area. We classified 1201 km (15 %) of these as main roads and considered the remaining 6627 km (85 %) as forest roads (Fig. 2). Our estimate of the total length of roads was 6 times higher than the 1304 km of roads from the GRIP database used in Carter et al. (2020). This resulted in a much larger percentage of our study area within 500 m, 1 km, and 3 km of a road. Median road density (linear km / km²) was 0.00 for both main roads and GLOBIO roads, but 0.26 when digitized forest roads were included with main roads. We summarize these descriptive statistics in Table 2.

Our GLM analyses of camera trap images of human use found low traffic volume for all traffic types; all models showed no lack of fit. Land management type (hunting lease or protected area) was the covariate with the largest coefficient in all models. Logging traffic was low and sporadic, occurring mostly closer to settlements ($p < 0.05$) and closer to main roads in hunting leases ($p < 0.01$). Rarely, camera sites had bursts of high logging traffic volume. Recreational traffic was low and variable across years, with median traffic volumes of 1 vehicle every 6–7 days. Covariate effects in hunting leases, though mostly significant ($p < 0.05$), were small (< 0.50). Spotlight poachers were rare, most often occurring in gentler terrain ($p < 0.05$). Coefficient estimates are provided in the Supplementary Information.

3.3. Tiger population density

Initial comparisons of the best detection model found that differences in sex for $g0$ and σ were much better supported than the null model according to AICc (Table 3). A detection model including sex and year effects on σ was slightly more supported than sex alone ($\Delta AICc = 2.268$); however, given the imprecision of the effects of year on σ and the fact that density estimates were almost identical to the model with sex effects only, we did not include year as a covariate.

Evaluation of the 13 univariate models of density found only habitat quality and a three km-buffer around main roads had coefficient estimates > 0.5 . We confirmed these variables were not correlated ($\chi^2 = 26.20$, $df = 2$, $p < 0.001$), then ran models with additive and interactive effects (Table 3). The top model included positive, independent effects of habitat ($\beta_{high\ quality} = 0.58$, 95 % CI [-0.23–1.39]) and areas at least three km from main roads ($\beta_{3km} = 0.75$, 95 % CI [-0.26–1.77]). This model predicted a tiger density of 0.27 tigers / km² (95 % CI [0.20–0.38]) in high-quality habitat at least three km from main roads (Fig. 3). The model with interactions between these covariates was not supported. The top two top covariate models only differed from the null density model in AICc by less than one, and all covariate effects were relatively weak (coefficients < 1) and with 95 % CIs often overlapping zero. Still, the likelihood-ratio test indicated that the inclusion of these covariates in the density model significantly improved upon the null density model if a more lenient p value was allowed ($\chi^2 = 5.28$, $df = 2$, $p < 0.10$).

Table 1

Summary of camera trap survey effort and captures of Amur tigers during four years of monitoring in Central Sikhote-Alin, Russian Far East. Each site typically consisted of two cameras, one on each side of a linear feature, to capture both sides of passing Amur tigers for individual identification. N indicated "number of", and "F:M" indicates the observed ratio of females to males.

Year	N sites	Trap nights	N individual tigers (F:M)	N total detections
2018–2019	111	8972	27 (15:12)	312
2019–2020	120	10,343	21 (11:10)	274
2020–2021	132	10,063	29 (16:13)	300
2021–2022	141	11,373	34 (18:16)	320
Total	504	40,751	69 (34:35)	1206

Table 2

Summary of road lengths, road densities, and percents of study area within varying buffer widths from roads. Road density is reported as linear km of road per km².

Road class	Total distance (km)	Road density median (range)*	Percent of study area within:		
			500 m	1 km	3 km
All roads	7828	0.26 (0.00–1.16)	25 %	42 %	73 %
Main roads only	1201	0.00 (0.00–0.90)	4 %	7 %	20 %
GLOBIO dataset**	1304	0.00 (0.00–0.23)	3 %	6 %	17 %

* Based on a 11 km-radius moving window (the average size of a female Amur tiger home range)

** Downloaded from GRIP roads database, used in analysis of Carter et al. (2020)

Table 3

Performance of 6 tested Spatial Capture-Recapture (SCR) models of Amur tiger density in Central Sikhote-Alin, Russian Far East. The number of parameters (“npar”), log likelihood (“logL”), AICc, difference in AICc from the top model (“dAICc”), and models’ AICc weights (“AICcwt”) are given in the remaining columns. Models 1 through 5 all include a “sex” covariate on the detection parameter of g0, and model 6 is included for comparison. “3-km main road” is the 3-km buffer along all main roads, while “habitat” is the binary variable of low- or high-quality habitat as described by Hebblewhite et al. (2014).

	model	npar	logL	AICc	dAICc	AICcwt
1	$D \sim 3\text{-km main road} + \text{habitat}$	8	-2254.39	4526.182	0	0.27
2	$D \sim 3\text{-km main road}$	7	-2255.56	4526.207	0.025	0.27
3	$D \sim 1$	6	-2257.03	4526.858	0.676	0.19
4	$D \sim \text{habitat}$	7	-2255.95	4526.993	0.811	0.18
5	$D \sim 3\text{ km main road} * \text{habitat}$	9	-2254.28	4528.335	2.153	0.09
6	$D \sim 1, g0 \sim 1, \sigma \sim 1$	4	-2413.82	4526.182	309.84	0.00

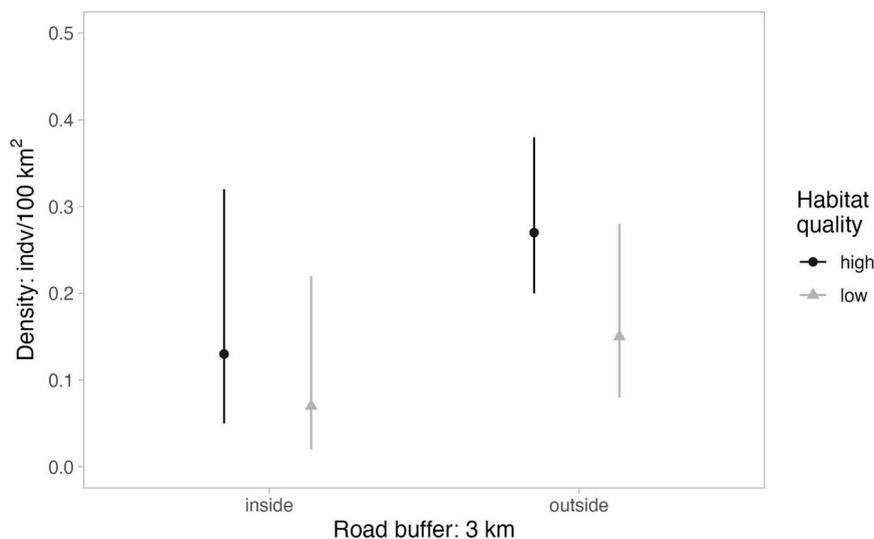


Fig. 3. Amur tiger density in Central Sikhote-Alin, Russian Far East, in response to 2 different spatial covariates: low and high quality habitat according to Hebblewhite et al. (2014); and inside or outside of a 3-km buffer from all roads. Error bars / shaded grey indicate 95 % confidence intervals.

3.4. Tiger survival, recruitment, and cub production

In our open SCR analyses of male tigers, a hazard half-normal function was more supported than the hazard exponential function to describe detection parameters ($\Delta\text{AICc} = 3.21$), and an exponential dispersal kernel with the scale parameter, α , estimated as 21.53 km (95 % CI [10.4–44.5]) best fit shifts in activity centers between years (Table 4), indicating median shifts in home range of 14.70 km per year and 90th percentile shifts of 49.51 km. The top model estimated low annual survival of male Amur tigers ($\varphi = 0.54$, 95 % CI [0.37–0.71]) and high recruitment with considerable variance ($f = 0.58$, 95 % CI [0.36–0.92]). The second-most supported model ($\Delta\text{AICc} = 0.88$) included higher survival of males with a greater proportion of detections outside of protected areas, though this relationship was imprecise and statistically insignificant (Fig. 4).

In contrast to males, the hazard exponential detection function was more supported for females than the hazard half-normal

Table 4

Model rank by AICc of 10 dispersal kernels for male and female Amur tigers in Central Sikhote-Alin, Russian Far East. The “movement kernel” describes different ways to model annual shifts in tiger activity centers between years. “npar” provides the number of parameters, “logLik” is the log likelihood, and “dAICc” and “AICcwt” provide the difference and weight of AICc values. Models for female tigers included a hazard exponential detection function, while models for male tigers used a hazard halfnormal function. No covariates were used on any parameter.

movement kernel	npar	logLik	AICc	dAICc	AICcwt
<i>Female Amur tigers</i>					
Exponential	5	-1441.83	2895.73	0.00	0.66
Bivariate t	6	-1441.46	2897.92	2.19	0.22
Gamma	6	-1443.64	2902.28	6.55	0.02
Independent	4	-1507.40	3024.12	128.39	0.00
Static	4	-1519.90	3049.14	153.41	0.00
<i>Male Amur tigers</i>					
Exponential	5	-1797.46	3607.14	0.00	0.94
Bivariate t	6	-1799.51	3614.24	7.11	0.03
Gamma	6	-1799.92	3615.06	7.93	0.02
Static	4	-1812.72	3634.87	27.73	0.00
Independent	4	-1828.43	3666.30	59.16	0.00

function ($\Delta\text{AICc} = 20.35$). Like male tigers, annual shifts in activity centers were best explained using an exponential bivariate distribution ($\alpha = 9.03$ km, 95 % CI [8.54–9.52]) (Table 4), with median shifts in home range of 6.23 km per year and 90th percentile shifts of 20.79 km. The top model ($\Delta\text{AICc} = 2.72$) estimated significantly higher annual female survival for tigers that were captured predominantly inside protected areas ($\varphi = 0.90$, 95 % CI [0.60–0.98]) rather than outside ($\varphi = 0.51$, 95 % CI [0.30–0.72]) (Fig. 4), but constant, high recruitment ($f = 0.47$, 95 % CI [0.29–0.79]).

Using a half-normal detection function with a covariate for sex, exponential dispersal kernel, and constant parameter estimates over time, we estimated a combined survival rate of 0.64 (95 % CI [0.52–0.75]), per capita recruitment of 0.48 (95 % CI [0.33–0.69]), and dispersal scale parameter of 12.60 km (95 % CI [8.51–18.85]). (Table 4).

The ratio of females with cubs to females without cubs was 2.3-times higher for tigers detected predominantly in protected areas (9:23) than those predominantly detected in hunting leases (4:24). Based on a Pearson’s chi-square test of homogeneity, this difference was not statistically significant ($\chi^2 = 1.69$, $df = 1$, $p = 0.19$).

3.5. Relationship between tiger persistence and vehicle traffic

We analyzed the *persistence* of tigers in 48 instances where they were captured in 2018–19 or 2019–20 and were detected in 1 + following years. The top logistic regression model included effects of *exposure* to logging traffic and sex ($\Delta\text{AICc} = 2.04$). This top model estimated the odds of *persistence* decreased by 92 % for every standard deviation increase in *exposure* to logging traffic ($\beta_{\text{logging}} =$

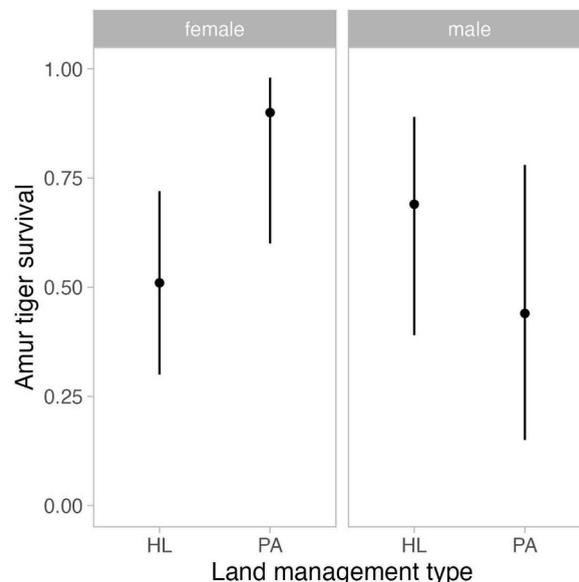


Fig. 4. Differences in estimated annual survival probability between adult male and female Amur tigers who were captured predominantly in hunting leases (HL) or protected areas (PA) in the Central Sikhote-Alin Mountains of the Russian Far East. Results are based on open spatial capture-recapture analyses of camera trap data over four years (2018–19–2021–22).

–2.58, 95 % CI [-5.94–0.78]), though this effect was imprecise and statistically insignificant ($p = 0.10$). The model seemed to fit the data reasonably well, as a Kolmogorov-Smirnov test for normality of residuals was insignificant ($p = 0.34$), and DHARMA tests of dispersion issues were all insignificant.

4. Discussion

In this study, we assessed Amur tiger population dynamics over a 4-year period and in a multiple-use landscape typical of much of the tiger's range in Russia. Most importantly, we found that protection of tigers from the cumulative disturbances of roads and human use – in the form of a strict nature preserve and national park – was critical to high annual survival of female tigers and greater cub production. However, these benefits did not appear to extend to male tigers, nor did they lead to population growth. Tiger density was higher when at least three km from the 1201 km of main roads. Though traffic levels on forest roads were very low relative to other places in Asia (e.g., India; Gubbi et al., 2012), and while we did not find a strong relationship between the density of all roads and tiger population density, the extensive network of 7828 km of roads, largely outside of protected areas, is cause for concern given the access they can provide to poachers (Clements et al., 2014; Laurance, 2001); 42 % of our study area was within one km of a road. We also found evidence that tigers living near places with high logging activity had greatly decreased odds of being detected in following years. These findings suggest that, even while tigers were offered sufficient refuge in protected areas to prevent population decline, tigers traveling outside of protected areas faced considerably heightened risks of human-caused mortality, potentially associated with logging, and facilitated by human access to roads. Given the low levels of female survival outside of protected areas, parts of the Sikhote-Alin without nearby protected areas may be unlikely to support sustainable populations of tigers.

These dynamics reflect source-sink characteristics expected for large carnivores in multiple-use landscapes (Balme et al., 2010; Benson et al., 2024; Newby et al., 2013; Woodroffe and Ginsberg, 1998). In our study area, female tigers with the majority of their detections inside protected areas had survival rates likely above the minimum of 0.85 identified by Chapron et al. (2008) to prevent population decline, while survival of females primarily outside protected areas were far below Chapron et al.'s threshold value. As our data suggest, the protected areas were sufficiently large to provide refuge for enough females to produce sufficient offspring to retain a low-density population across the entire landscape. Yet, male tigers did not appear to receive such benefits, as there were no significant differences in survival between males captured predominantly inside or outside of protected areas. Robinson et al. (2015), who reported on survival rates of tigers primarily captured within Sikhote-Alin Reserve, reported higher survival rates for males than in our sample from a multiple-use landscape that included the same reserve. We hypothesize male tigers were more susceptible to human-caused mortality than females because most individuals likely spent large proportions of time beyond reserve boundaries (Goodrich et al., 2010; Kaplanov, 1948; Yudakov and Nikolaev, 2012). While the persistence of tigers in our study area itself is a conservation success, we caution that the high risk of mortality for males and females outside of protected areas likely reduces dispersal success (Newby et al., 2013) and prevents the full recovery of the tiger population across the landscape, as has been found for other large carnivores in multiple-use landscapes (Balme et al., 2010; Cassidy et al., 2024; Hebblewhite and Whittington, 2020; Linkie et al., 2006).

We expected density of all roads to be a strong predictor of tiger density, as we hypothesized more roads outside of protected areas would mean greater access for poachers, and other studies have identified a negative relationship between carnivores and road densities (Lamb et al., 2018). Instead, we found some evidence that tiger density was twice as high in areas at least three km away from main roads, though we caution that the coefficient estimate was relatively weak (<1) and had high relative standard error (68 %). Vehicle traffic on forest roads may have been too low to elicit an avoidance response, unlike further south near the Sino-Russian border (Xiao et al., 2018). Kerley et al. (2002) documented how tigers closer to the main road bisecting the coastal section Sikhote-Alin Biosphere Reserve faced high human-caused mortality. Oleynikov et al. (2025) confirmed this region has continued to be a hotspot for tiger-vehicle collisions. Poaching also has been documented as a persistent main cause of tiger mortality in our study area (Goodrich et al., 2008; Robinson et al., 2015), and the low survival rates we estimated for both male and female tigers outside of protected areas suggests this threat continues. It is unclear in our study if the lower observed tiger density closer to main roads was due to tigers avoiding those areas, persistent poaching, or both. Snow tracking of individual tiger movements in the region and monitoring of vehicle traffic volumes on main roads could help illuminate the mechanisms by which main roads are affecting tigers.

In our analysis of the human use of forest roads, tiger persistence was not influenced by general traffic (e.g., personal vehicles) nor by spotlight poachers (cf. Skidmore, 2021) observed on forest roads. But places with short, intense levels of logging traffic greatly reduced the odds of tigers being detected for 2 + years. With logging operations, there is a high concentration of people and therefore more chances for at least one of them to try and poach tigers. Past research has documented how logging trucks are sometimes used to hide and transport poached Amur tiger parts (Skidmore, 2021). It is therefore not a stretch to assume that tigers in our study with high exposure to logging-related activity and not detected in later years were poached.

Differences in protected vs multiple-use landscapes could affect tiger populations in ways beyond what we evaluated here, especially through the availability of preferred prey (Miquelle et al., 2010). Our study design did not allow for accurate estimates of prey abundance, which are notoriously difficult to obtain (Waller et al., 2024). Still, there is evidence of differences in prey abundance between protected areas and adjacent lands (Matiukhina et al., 2010). The population dynamics of tigers are no doubt impacted by both variation in probability of poaching and prey levels across this landscape, and we encourage future research to investigate this variation.

Our study provides an example of how a single camera trap monitoring system, with sufficient camera trap density and study area size, can provide valuable information on multiple demographic processes. Many camera trap studies focus only on population density (reviewed by Palmero et al., 2023). But without considering other parameters like survival, reproduction, and emigration, the drivers

of population growth or decline may be missed (Harihar et al., 2020). Several past studies have analyzed tiger apparent survival, but non-spatial capture-recapture analyses did not allow them to differentiate between survival and emigration (Bisht et al., 2019; Duangchantrasiri et al., 2024; Dutta and Krishnamurthy, 2024; Harihar et al., 2020; Karanth et al., 2006; Majumder et al., 2017). Because our study area was considerably larger than the estimated shifts in tiger activity centers between years, and given the density of camera traps, we believe our study design and open SCR analysis captured the process of dispersal and allowed the models to separate emigration from mortality (Efford and Schofield, 2022; Gardner et al., 2018). This was critical to investigating covariates related to tiger survival specifically. And though not a focus of this research, the explicit modeling of dispersal provided insights into Amur tiger movement behavior: the negative exponential movement kernel was best supported for both male and female Amur tigers, meaning most animals did not move their home ranges very far between years, yet a few had considerable shifts. Further analysis of these shifts could indicate the status of individuals in the population – whether resident, “floater”, or transient. The expected dispersal rates could also inform natural recolonization rates of Amur tigers into suitable habitats that are currently largely uninhabited, such as the Lesser Khingan Mountains in northeast China (Yachmennikova et al., 2023).

5. Conclusions

Despite the success of protected areas in supporting female survival and greater cub production, our estimated tiger density was the same as the baseline density identified in Harihar et al. (2018). Six years later, this is still far from the recovery target of at least 0.63 tigers / 100 km² in our study area identified by Harihar et al., or from the more ambitious goal of 1.00 tigers / 100 km² set by Hötte et al. (2016). The rescue effect of protected areas was sufficient to ensure tigers were retained in protected areas and in adjacent multiple-use lands but was not sufficient to drive a recovery of tigers across the Central Sikhote-Alin landscape. Despite very low traffic rates on forest roads, the reality is that rare poaching events (of prey as well as tigers) have resulted in a greatly depressed population of tigers across a large landscape. This supports the arguments of Wikramanayake et al. (2011) that a more comprehensive approach to tiger conservation is needed to recover the species.

We reiterate the conclusions of Carroll and Miquelle (2006) that to support Amur tiger population recovery – beyond just persistence – more investments are needed in law enforcement both in surrounding hunting leases as well as protected areas where tiger numbers were significantly greater in the past (Miquelle et al., 2015). Logging companies could play a key role in discouraging poaching and other illegal activities of their employees as part of this greater investment in law enforcement. These conclusions echo earlier calls for reduced poaching levels across northeast Asia as a foundation for better wildlife management, including both tigers and prey (Goodrich et al., 2008; Hötte et al., 2016; Qi et al., 2021; Soh et al., 2014).

CRedit authorship contribution statement

Scott J. Waller: Conceptualization (equal), methodology (equal), funding acquisition (supporting), project administration (equal), investigation (equal), data curation (supporting), formal analysis (lead), writing – original draft (lead), writing – review and editing (lead). **Aleksandr N. Rybin:** methodology (supporting), project administration (equal), investigation (lead), data curation (equal), writing – review and editing (supporting). **Ekaterina I. Nikolaeva:** data curation (lead), writing – review and editing (supporting). **Anton V. Semyonov:** Conceptualization (supporting), methodology (supporting), investigation (supporting), data curation (lead), writing – review and editing (supporting). **Svetlana V. Soutyrina:** Methodology (supporting), investigation (supporting), data curation (supporting), writing – review and editing (supporting). **Jonathan C. Slaght:** Conceptualization (supporting), funding acquisition (supporting), supervision (supporting), writing – review and editing (supporting). **Ivan V. Seryodkin:** Methodology (supporting), project administration (supporting), writing – review and editing (supporting). **Dale G. Miquelle:** Conceptualization (equal), methodology (equal), funding acquisition (lead), supervision (lead), investigation (supporting), formal analysis (supporting), writing – original draft (supporting), writing – review and editing (supporting).

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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.

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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.2026.e04099](https://doi.org/10.1016/j.gecco.2026.e04099).

Data availability

Our data concerns an Endangered species including in Russian federal protected areas. As such, we cannot make our data publicly available. Any inquiries can be sent to the corresponding author.

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