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Rehabilitating tigers for range expansion: lessons from the Russian Far East

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ABSTRACT Empty but suitable habitat exists for many of the world's terrestrial large carnivores, yet reintroductions are often considered difficult. In the Russian Far East, orphaned Amur tiger (*Panthera tigris altaica*) cubs were brought into captivity but prepared for re-release into the wild. We addressed 2 questions after reintroduction: 1) were individuals raised in captivity capable of killing prey at a rate sufficient to survive, and 2) did individuals avoid use of domestic animals as a primary source of food? We collected data on hunting behavior of 6 orphaned tigers re-released into their indigenous range, and compared kill composition, kill rate, and consumption rate to individuals studied within the existing range (Sikhote-Alin) of Amur tigers. Prey composition of rehabilitated tigers varied from that of the Sikhote-Alin tigers, but composition of major food groups was nearly identical. Kill rate of rehabilitated tigers was higher and prey size was smaller than that of Sikhote-Alin tigers, but consumption rates were nearly identical. One young male tiger depredated domestic animals, but other individuals only rarely preyed on dogs or cattle they encountered in forests. We documented high survival, reproduction, and recruitment of re-released individuals. These results indicate that tigers held in captivity during the majority of their early lives can survive in the wild, so long as exposure to humans is kept to a minimum and individuals learn to hunt wild prey before release. Results provide a potential framework for reintroductions of tigers and other large felids across the globe.

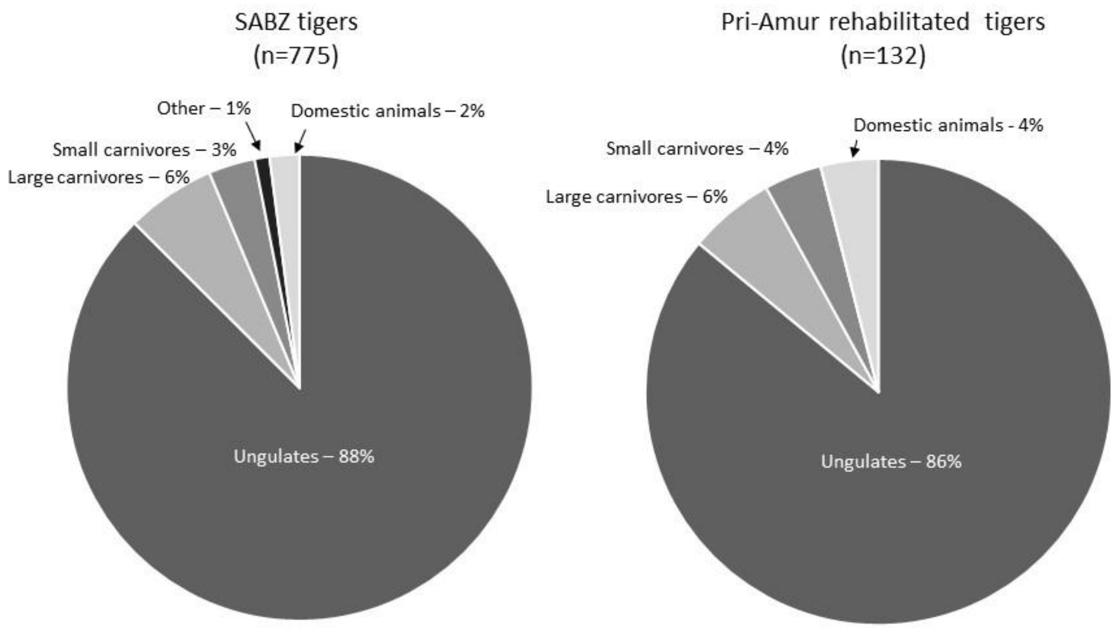
(Russian language title and abstract follows)

Реабилитация тигров для расширения их ареала: опыт на Дальнем Востоке России

АБСТРАКТ Для многих крупных территориальных хищников существует пригодное для обитания, но еще не заселенное пространство, однако внедрение программ реинтродукции для увеличения численности этих животных считается сложной задачей. На Дальнем Востоке России тигрята, оставшиеся без матери, содержались в неволе перед последующим возвращением в их исторический ареал. После реинтродукции тигрят-сирот были исследованы два вопроса: 1) способны ли особи, выращенные в неволе, добывать животных с частотой достаточной для выживания? и 2) будут ли они избегать контактов с людьми и охоты на домашних животных? Была собрана информация об охотничьем поведении шести тигрят-сирот, реинтродуцированных в исторический ареал амурского тигра, и проведено сравнение рациона, частоты добычи жертв и уровня потребления с данными, полученными от особей, исследованных в современном ареале (Средний Сихотэ-Алинь) амурских тигров. Видовой состав рациона реинтродуцированных тигров и тигров Среднего Сихотэ-Алиня значительно различался, однако состав рациона по группам добычи был практически идентичен. Частота добычи жертв реинтродуцированных тигров была выше, а размер добычи – меньше по сравнению с тиграми из Среднего Сихотэ-Алиня, однако уровни потребления оказались схожими. Хотя один молодой реинтродуцированный самец охотился на домашних животных, другие особи редко нападали на собак или сельскохозяйственных животных, с которыми они сталкивались в дикой природе. У реинтродуцированных особей зафиксирован высокий уровень выживания, размножения и восполнения. Эти результаты показывают, что тигры, находившиеся в неволе в течение большей части своего ювенильного периода, способны успешно адаптироваться к дикой природе, при условии, что в период реабилитации особи обучаются охоте на диких животных, а контакт с человеком сведен к минимуму. Полученные результаты могут послужить основой для проведения реинтродукции крупных кошачьих, выращенных в неволе в различных регионах мира.

Graphical abstract

We assessed whether orphaned Amur tiger cubs, raised in captivity and released back into the wild, could adequately acquire wild prey and avoid use of domestic animals. Cubs were raised with minimal human contact and provided live, wild prey throughout their time in captivity. Upon release, consumption rate of tigers was similar to that of other Amur tigers in wild, with a similar focus on large ungulates as the primary prey. One released animal killed domestic animals and was re-captured. The other 5 tigers thrived in the wild, providing a potential framework for reintroductions of tigers and other large felids across the globe.



KEYWORDS Amur tiger, diet composition, kill rate, *Panthera tigris*, reintroduction

Reintroduction, restoration, or rehabilitation and release of large carnivores are considered difficult tasks with major risks. Yet as populations of large carnivores decline in size and distribution, the calls for reintroductions increase (Wolf and Ripple 2018). Apparently suitable but uninhabited landscapes for large carnivores may be relatively abundant. For instance, it has recently been determined that tiger (*Panthera tigris*) distribution could increase by as much as 50% by restoring tigers to suitable but uninhabited landscapes across Asia (Sanderson et al. 2023, Gray et al. 2023). Yet release of large carnivores back into the wild is nearly always controversial because they are often perceived as a threat to humans (Hebblewhite et al. 2011, Johansson et al. 2016).

Although the topic of large carnivore reintroductions is often approached cautiously (Johnsingh and Madhusudan 2009, Jackson and Ale 2009, Kelly and Silver 2009), reintroductions are occurring and seem to be getting more common, especially for large felids (Hayward and Somers 2009, Becker et al. 2022, Miquelle et al. 2024).

There are approximately 4,500 tigers remaining in the wild in Asia (Goodrich et al. 2022), occupying only 8% of their indigenous range (Sanderson et al. 2023). In northeast Asia, Amur tigers (*P. t. altaica*) range over a large landscape (approximately 180,000 km^2; Hebblewhite et al. 2014, Qi et al. 2021), but much potential habitat (Sanderson et al. 2023) is uninhabited. In the Pri-Amur region, tigers originally occurred along both sides of the Amur River: in Amur Oblast and the Jewish Autonomous Oblast (JAO) in Russia, and in the Lesser Khingan Mountains of China's Heilongjiang Province (Heptner and Sludskii 1992, Yachmennikova et al. 2023). Tigers in these areas were largely extirpated in the 1950s through the 1970s. Since then, dispersing males from the Sikhote-Alin Mountains were regularly documented in the Pri-Amur area (Kolobaev et al. 2005, Yachmennikova et al. 2023), but no breeding population had developed.

One continuing aspect of the human–tiger interface in Russia is the occasional appearance of young, abandoned cubs. Although the exact cause of abandonment is not usually known, we suspect that females with cubs are more likely to stand their ground to defend cubs from approaching humans, making them more vulnerable to poaching, which is the primary source of mortality for Amur tigers (Goodrich et al. 2008, Robinson et al. 2015). In the past, young cubs without a mother were usually taken into custody and shipped to zoos (Spitsin et al. 1987, Yudakov and Nikolaev 2012).

In 2012 the A. N. Servetsov Institute of Ecology and Evolution, of the Russian Academy of Sciences, completed construction of a tiger rehabilitation center in the Russian Far East in time to receive a female cub orphaned at approximately 4 months of age (Rozhnov et al. 2021). In 2013, 5 more tiger cubs arrived at the facility, all 3-5 months of age (Rozhnov et al. 2018). Since then, the Amur Tiger Center has overseen the rehabilitation of at least another 9 tigers (ANO Tiger Annual Reports: https://amur-tiger.ru/en/library?filter=cat-4, accessed 29 May 2022). Instead of sending these cubs to zoos or releasing them back into the remaining tiger population in the Sikhote-Alin Mountain Range, it was decided to use the majority of these tigers (n = 13) to recolonize the Pri-Amur region. A preliminary assessment indicated prey densities were sufficiently high and the potential for tiger–human conflict at least as low as in the tiger's current range (V. V. Aramilev, Pacific Institute of Geography, Russian Academy of Sciences, unpublished report number 0123200000313002189 [In Russian]).

In this study, we sought to answer 2 questions to help assess the success of this reintroduction effort: 1) would tigers born in the wild but raised in captivity without support or training by a mother become sufficiently proficient in hunting wild prey to survive and reproduce in the wild, and 2) would these tigers adequately avoid use of domestic animals as a source of food? We collected data on hunting behavior and kill composition of 6 reintroduced tigers that were reared in captivity after the loss of their mother in the wild. We report on kill composition, kill rates, and consumption rates after release and compare these results to similar data from wild tigers in and around Sikhote-Alin Biosphere Reserve in the central Sikhote-Alin Mountains (Miller et al. 2013). While there were differences in relative prey abundance between the sites where cubs were released and the area where naturally occurring tigers were monitored in Sikhote-Alin, we assumed that the composition of major categories of prey, kill rates, and biomass consumption rates would provide indications of how capable rehabilitated tigers were at sustaining themselves on wild prey. Through this analysis, our goal was to accurately document predation patterns of these rehabilitated tigers as one measure of the success of this reintroduction attempt.

STUDY AREA

The 6 tigers included in this study were crated and carried to 1 of 3 release sites in the Pri-Amur region of the Russian Far East (Figure 1), an area west of the current primary tiger range (in the Sikhote-Alin Mountains) but within the historical range of tigers in Russia (Heptner and Sludski 1992). Human densities in both areas are low, ranging from 10.98 people/km^2 in Primorskii Krai to 1.62 people/km^2 in Khabarovskii Krai, which together encompass the Sikhote-Alin tiger population, and from 2.08 people/km^2 in Amur Oblast to 4.02 people/km^2 in Jewish Autonmous Oblast, which together encompass the Pri-Amur region (Rosstat 2022). Both regions have some of the lowest human footprints within tiger range in Asia (Sanderson et al. 2023).

The Pri-Amur region is composed of extensive wetlands draining into the Amur River interspersed with hilly uplands, which represent suitable tiger habitat. Vegetative species composition and habitat characteristics for tigers in the uplands of the Pri-Amur and central Sikhote-Alin Mountains are similar (see Miquelle et al. 2010 for descriptions). Red deer (*Cervus elaphus*) are relatively scarce across much of the Pri-Amur region but are much more common in the central Sikhote-Alin Mountains; sika deer (*Cervus nippon*) are absent in the Pri-Amur but locally abundant in the central Sikhote-Alin; and roe deer (*Capreolus pygargus*) and wild boar (*Sus scrofa*) are common (with wild boar relatively abundant in suitable conditions) at both sites. Moose (*Alces alces*) are more common in the Pri-Amur region than in the central Sikhote-Alin Mountains. Brown bears (*Ursus arctos*) and Asian black bears (*U. thibetanus*) occur in the Pri-Amur and Sikhote-Alin Mountains. In the Pri-Amur, wolves (*Canis lupus*) are common, while in the Sikhote Alin, especially where tigers are common, they are rare (Miquelle et al. 2005*b*). Raccoon dogs (*Nyctereutes procyonoides*) and badgers (*Meles leucurus*) were common in both areas.

METHODS

Tiger rehabilitation and release

Details of rehabilitating and preparing cubs for release into the wild are provided by Blidchenko et al. (2015) and Rozhnov et al. (2018, 2021). In brief, abandoned cubs were brought into captivity between 3 and 6 months of age (Rozhnov et al. 2021) after it was clear that no adult female was associated with the cubs for multiple days. They were kept in quarantine facilities for the first month and then moved to an enclosure, either alone or in association with littermates or other similarly aged individuals. Enclosures (0.3-0.7 ha) were built of chain-link fencing 4.5 m high with an inward overhang of 1 m at the top (Rozhnov et al. 2021). Natural vegetation was retained in the enclosures, but the degree of cover varied in each, from largely forested with brushy undercover to mostly open tall grass fields. All efforts were made to minimize contact with humans: material was placed on the chain-link fence to eliminate visual contact with humans, animals were observed only via a network of remote video cameras set up around each enclosure, and food was provided via cages that were built into the fencing so that food and prey could be placed in a small cage and then released at a later time (to minimize chances that tigers would relate human activity to the presentation of food and prey).

Tigers were fed almost exclusively wild game, although the first cub was fed some beef. When cubs were 7-8 months of age, small live prey (domestic rabbits and pheasants) were presented to them. When cubs reached 11 months of age, live young wild boar and young sika deer were released into the pens. Larger prey (subadult or adult wild boar and sika deer) were released into pens to tigers older than 15 months of age after their permanent teeth were fully developed. For the 6 months prior to release, tigers were provided only live natural prey items and were therefore wholly dependent on their own abilities to capture prey. Live prey were released into pens at intervals ranging from 7 to 12 days. Each cub had successfully killed at least 24 wild boar or sika deer before it was considered ready for release (Blidchenko et al. 2015). Before release, all cubs had to meet minimum criteria associated with hunting proficiency, human avoidance, and interactions with conspecifics, using similar criteria to those developed for Persian leopards (*Panthera pardus tulliana*; Rozhnov et al. 2020).

Tigers were released when they were 18 months of age (average age of dispersal in the wild; Kerley et al. 2003) or shortly afterwards. All efforts were also made to release cubs in late spring, when the emergence of small carnivores from hibernation (e.g., badgers and raccoon dogs) and the birth of young ungulates ensured the most abundant and most vulnerable individuals would be available as prey.

Estimating number of kills, kill composition, and kill size

Before animals were released back into the wild, they were anesthetized, given a medical evaluation, and fitted with global positioning system (GPS) collars. The first deployed collar (Lotek Argos-GPS, Newmarket, Ontario, Canada) was scheduled to acquire 6 GPS locations per day. All others were Lotek Iridium-GPS collars scheduled to transmit 24 locations per day, on the hour, and transmit data every 12 hours via the Iridium satellite system (Rozhnov et al. 2019, 2021).

Methods to find kills of tigers in the central Sikhote-Alin Mountains are described by Miller et al. (2013) and a similar approach was applied to the Pri-Amur region, with the following nuances. We found kills made by the first tiger released using a combination of checking clusters of locations in summer and then, after her collar failed, by snow-tracking her movements during the winter months (Yudakov and Nikolaev 2012). For the other 5 individuals, we investigated clusters of GPS-collared tiger locations to determine the presence or absence of kills. After uploading GPS data, we used a Python script (Python Software Foundation, Hampton, NH, USA) developed by Knopff et al. (2009) to identify potential kill sites as clusters of 2 or more locations within 100 m and 48 hours of each other. We confirmed presence of kills by physically searching 50-100 m around each location in a cluster. During winter, we approached potential kill sites identified with the Python script and then, once in the vicinity, followed tracks in the snow to find kills. During snow-free months, we relied solely on GPS data downloads and more extensive searches of cluster sites. We attempted to visit clusters during each quarter of the calendar year multiple times. We primarily focused on large clusters where tigers had spent 10 or more hours, but we also investigated small clusters and single locations to attempt to locate kills of small prey. Following tracks in snow provided additional opportunities to search for smaller kills that might not show up from searches of large clusters.

We compared kill composition and kill size data from these 6 translocated tigers in the Pri-Amur region to all data collected from 37 radio-collared tigers in and around Sikhote-Alin Zapovednik from 1992 through 2013 (Miquelle et al. 2010, Petrunenko 2021). To facilitate comparisons while acknowledging variations in relative abundance of prey species between the Pri-Amur and Sikhote-Alin sites, we grouped prey species into 5 prey types, defined as wild ungulates (moose, red deer, sika deer, roe deer, musk deer [*Moschus moschiferus*], and wild boar), large carnivores (brown and Asian black bears, wolves, and tigers), small carnivores (badgers, raccoon dogs, red fox [*Vulpes vulpes*]), other wild prey (seals [*Phoca* spp.] and birds), and domestic species (cows, horses, and dogs), and compared the relative contributions of these groups to the diet of Pri-Amur and Sikhote-Alin tigers. To estimate relative contribution of biomass to the diet, we multiplied the number of adult male, adult female, and young (<1 year) of each species that were killed by total live weights from the literature (derived from Bromley and Kucherenko 1983, Danilkin 1999, and Miller et al. 2013; Table S1, available in Supporting Information). Where sex of the kill could not be determined, we used the average weight of adult females and males, and if age of the prey individual could not be determined, we assumed it was an adult.

To estimate kill rates and consumption rates of tigers, we first needed to predict the total number of kills made by tigers during our period of analysis, beyond the kills verified in the field. To do this, we used the GPSeqClus package (Clapp et al. 2021) in Program R (R Core Team 2023) to identify clusters of locations representing potential kill sites for both the Pri-Amur dataset and the Sikhote-Alin dataset collected by Miller et al. (2013). Using the subset of clusters that had been searched for evidence of a kill, we then used a multiple logistic regression analysis (Hosmer and Lemeshow 2000, Anderson and Lindzey 2003) for each of the 2 groups of tigers to model the probability of a cluster being an actual kill site. Following Miller et al. (2013), we used a combination of 6 potential explanatory variables: 1) the number of hours between the first and last location of a cluster (hours), 2) the number of 24-hour periods between the first and last location of a cluster (days), 3) a binary variable indicating whether a tiger spent more or less than 24 hours at a cluster (multi-day), 4) the fidelity of the tiger to the cluster site, measured as the proportion of locations for the duration of a cluster that were within the cluster (fidelity), 5) the distance between the center of a cluster and its farthest point (radius), and 6) the average distance of all locations within the cluster to its center (average distance). We used these variables to predict the probability of a cluster being a kill site using the standard logistic regression equation (Hosmer and Lemeshow 2000):

$$\Pr(kill) = \frac{e^{\beta_0+\beta_1 X_1+\beta_2 X_2 \dots +\beta_n X_n}}{1+ e^{\beta_0+\beta_1 X_1+\beta_2 X_2 \dots +\beta_n X_n}},$$

where β_0 is the intercept, β_i is the estimated coefficient of the effect of variable X_i on the probability of a cluster being a kill, and *n* is the total number of explanatory variables used in the model. Because our aim was to maximize the predictive capability of our models, we used the MuMIn package in R (Bartón 2020) to perform a stepwise regression procedure with backward elimination to identify the best-supported models to predict kills based on Akaike's Information Criterion for small sample size (AIC$_c$; Burnham and Anderson 2002). We then applied the top models to the entire dataset of Pri-Amur and Sikhote-Alin tigers to assign each cluster a probability of being a kill site, including those clusters that were not investigated in the field.

To determine the total predicted number of kills, we converted the estimated probabilities of clusters to either a kill or non-kill site by choosing cut-off values with the greatest sums of sensitivity and specificity (Hosmer and Lemeshow 2000). We then used receiver operating characteristic (ROC) curves to evaluate how this cut-off value balanced the true positive rate (i.e., sensitivity, or the proportion of true kill sites that were predicted to be kill sites) with the false positive rate (i.e., 1 – specificity, or the probability of a Type 1 error). We used the area under the ROC curve (AUC) as an index of classification accuracy and as a final assessment of the classification of our top models. To conduct this analysis of cut-off values with ROC curves and obtain estimates of AUC, we used the ROCR package in R (Sing et al. 2005).

Estimating kill and consumption rates

We estimated kill and consumption rates of rehabilitated tigers released into the Pri-Amur region and recalculated the same values from wild tigers studied in Sikhote-Alin by Miller et al (2013) using a slightly revised and updated dataset of kills.

We estimated kill rates using the ratio estimator (Hebblewhite et al. 2003):

$$\hat{\beta} = \frac{\sum_{i=1}^{n} y_i}{\sum_{i=1}^{n} x_i},$$

where $\hat{\beta}$ is the estimated kill rate of individual tigers, i represents each individual of the total number of tigers n, and y is the total number of predicted kills for tiger i during the time x that tiger i was sampled. We estimated the variance of kill-rates using the standard formula described in Hebblewhite et al. (2003):

$$\widehat{var}(\hat{\beta}) = \frac{\sum_{i=1}^{n}(y_i - \hat{\beta} x_i)^2}{\bar{x}^2 n(n-1)},$$

where $\bar{x}$ is the average amount of time each tiger was sampled. Because we continuously monitored each tiger and estimated kill rates for the entire year, the term $\left(1-\frac{x}{X}\right)$, which is meant to account for inconsistent sampling during the sampling period, drops out of equation (2) in Hebblewhite et al. (2003) for our analysis (M. Hebblewhite, University of Montana, personal communication).

We converted kill rates to consumption rates by multiplying the estimated kill rates (kills per day) and their associated errors by the estimated amount of biomass consumed at each kill (kg per kill; Miller et al. 2013). We assumed that the field-verified kill sites of Sikhote-Alin and Pri-Amur tigers within the study periods were a representative sample of species and sex-age composition for all kill sites for each group of tigers. This sample was restricted to only the period of kill rate analysis, which is considerably smaller than our sample to estimate kill composition for Sikhote-Alin tigers (described above). To estimate the biomass consumed at each kill, we used a 2-stage process that first estimated the average consumable weight of each species, then converted these weights to the total biomass consumed at each kill. In the first stage, we converted the sex- and age-specific live weights (Table S1) to consumable biomass (kg), assuming 68% and 79% of the total weight of large and small prey, respectively, was consumable, and further assuming that 15% of this consumable weight was lost to scavengers (following Miller et al. 2013). We then adjusted these sex- and age-specific consumable weights by the proportion that each sex- and age-class contributed to all kills of that species, then added them together for a final, average consumable weight for that species. In the next stage, we multiplied these species-specific consumable weights by the number of field-verified kills of that species for the total biomass consumed of each species in our sample. This allowed us to then estimate the proportion of biomass each species contributed to our sample of kills. Finally, we multiplied these proportions by the average consumable weight of each species (estimated in the first stage) to derive an average biomass consumed per kill. Results are presented as mean ± standard error.

RESULTS

Release of rehabilitated tigers into the Pri-Amur region

The first tiger was released into the Pri-Amur region into Bastak Reserve on 9 May 2013, and 5 more GPS-collared tigers (2 females, 3 males) were released in May-June 2014 (Figure 1). The collar of the first female failed on 29 August 2013 (113 days); data from the other 2 females were collected for 350 and 811 days. The 3 males were tracked for 205, 273, and 1087 days, respectively. We obtained 4,700–25,632 locations from each tiger, for a total of 63,616 locations. The 3 females tended to remain near release sites (2 retained the release site as part of their territory, 1 moved approximately 100 km southeast before settling within Khinghanskii Reserve). Males mostly roamed widely after release, including extensive forays into China by 2 males (Rozhnov et al. 2021).

We identified 4,654 unique clusters representing potential kill sites. Teams searched for kills in 19 of the 29 months when GPS collars were functional on tigers in the Pri-Amur between May 2013 and April 2016. Teams investigated a minimum of 348 clusters with 132 kills identified, but we used only 113 to estimate kill rates (long intervals between locations made data from the first collared tiger incompatible for this analysis). We were unable to search clusters of tigers that moved into China but received reports on their activities from colleagues there (which are reported here but not included in our kill data set). We compared kills identified in the Pri-Amur region with kills from the central

Sikhote-Alin study area, where we documented 714 kills by 37 radio-collared tigers over 22 years (Petrunenko 2021).

Diet composition

Variations in the kill composition between these 2 areas largely reflected variation in relative abundance of potential prey species. Wild boar were the most abundant large ungulate in the Pri-Amur and represented 55% of the kills we found there (Table 1). The majority of wild boar killed (67%) were <2 years old. In the central Sikhote-Alin Mountains, wild boar represented only 25% of the kills reported over a 20-year period. However, Miller et al. (2013) reported 67% of wild boar kills were <2 years old, exactly the same percentage as in the Pri-Amur. Roe deer were the second most abundant ungulate in the Pri-Amur, and were the second most common species taken (23.5%) by rehabilitated tigers (Table 1), while in central Sikhote-Alin they accounted for only 9% of the kills (Table 1). Red deer, which were rare in the Pri-Amur, accounted for only 3% of the kills observed but were the most common prey species (43%) found in central Sikhote-Alin. Sika deer are not found in the Pri-Amur but represented 9% of kills reported in central Sikhote-Alin. Moose are exceedingly rare in central Sikhote-Alin, especially in the primary study site, and hence only one kill of moose was found there, while we discovered 5 kills of moose by rehabilitated tigers in the Pri-Amur (all young or subadults). Even though rehabilitated tigers had never encountered moose, bears, or wolves, at least during captivity, they recognized and successfully subdued them as prey.

Large carnivores were not a large proportion of the kills made by tigers in the central Sikhote-Alin, but they were killed by tigers (Table 1). Similarly, in the Pri-Amur we found 3 bears (2 brown bears and 1 Asiatic black bear) killed by rehabilitated tigers; 2 of these were <2 years old, and the age of the third bear could not be determined. In Sikhote-Alin, wolves are exceedingly rare and were never recorded as a kill by tigers, but in the Pri-Amur region 5 wolves were killed, all by female tigers that had already established territories. Small carnivores (mostly badgers and raccoon dogs) made up a small percentage of the kills (3-4%) found in both locales.

Domestic animals comprised a small percentage of the kills made by tigers in both areas (3.8% in the Pri-Amur, 2.0% in Sikhote-Alin). Dogs and cows were taken in both areas in forests, but collared tigers did not enter villages to prey on domestic animals in either area. However, one of the males that crossed into China killed multiple domestic animals, including over 13 goats killed in a single event. When this individual returned to Russian territory, it failed to demonstrate adequate fear of humans. Consequently, this tiger was captured and placed in a Russian zoo (Dudina et al. 2019). All other individuals rehabilitated and released into the wild relied primarily on wild species as prey, and none were reported to be in conflict with humans. Grouping prey species into 5 major categories (ungulates, large carnivores, small carnivores, domestic animals, and other), the distribution of kills made by rehabilitated tigers was remarkably similar to that made by tigers in Sikhote-Alin (Figure 2), indicating similar patterns of prey selection with prey availability likely explaining species-specific variation.

Kill and consumption rates

Over 2 years (2010-2011), Miller et al. (2013) tracked 3 GPS-collared adult tigers in and around Sikhote-Alin Zapovednik for 98, 416, and 310 days for 1 male and 2 females, respectively, obtaining 1,529–4,644 locations from each tiger for a total of 9,161 locations. Our calculations identified 972 unique clusters representing potential kill sites.

Our best logistic regression model differentiating kill sites from other clusters (Table 2) indicated that the probability a cluster contained a kill increased with the number of days at the site (β = -1.300 ± 0.585; *P* < 0.026), hours at the site (β = 0.094 ± 0.023; *P* < 0.001), with increased site fidelity (β = 3.857 ± 0.808; *P* < 0.001), and when tigers were present at a cluster for multiple days (β = 1.260 ± 0.576; *P* = 0.029). The counter-intuitive negative β value for number of days at site was likely due to collinearity correlations with other variables but is reported as part of the best predictive model. The model accurately classified clusters as kill or non-kill sites with an AUC of 0.84. The optimized probability cutoff to determine probable kill sites was 0.328, which corresponded to an overall classification success of 85.2%. Our best model predicted 117 kill sites, representing 12% of all clusters (117/972), including the 113 kill sites we identified (97%).

Our best logistic regression model for differentiating clusters that contained tiger kills from non-kill clusters of rehabilitated tigers in the Pri-Amur region (Table 2) included hours spent at a site (β = 0.021 ± 0.008; *P* = 0.005), average distance of all locations from the cluster center (β = 0.022 ± 0.013; *P* = 0.073), and when tigers spent multiple days at a cluster (β = 2.003 ± 0.471; *P* < 0.001). The model fit the data well with area under the curve 0.86. The best probability cutoff for which we considered a cluster a probable kill site was 0.437, which corresponded to an overall classification success of 80%. Our best model predicted 553 kill sites, representing 12% of all clusters (553/4,654), of which we confirmed 102 (18%) of them in the field.

We predicted 117 kills over 830 days for Sikhote-Alin tigers and 553 predicted kills over 2,726 days for tigers released in the Pri-Amur region. Using the ratio estimator and variance calculation, we found that the kill rate of Sikhote-Alin tigers (0.14 ± 0.01 kills/day) was less than that of rehabilitated tigers (0.20 ± 0.01 kills/day; Figure 3A). However, Sikhote-Alin tigers killed larger prey than rehabilitated tigers, with an average live prey weighing 76.1 kg/kill versus 54.9 kg/kill for rehabilitated tigers. As a result, wild tigers consumed more biomass at each kill (Figure 3B), averaging 58.0 kg/kill compared to 39.2 kg/kill consumed by Pri-Amur tigers. These differences in kill rates and prey size between Sikhote-Alin and Pri-Amur tigers counterbalanced each other, resulting in similar consumption rates between Sikhote-Alin and Pri-Amur tigers (Fig. 3C): 8.24 ± 0.70 kg/day for Sikhote-Alin tigers, and 7.96 ± 0.58 kg/day for Pri-Amur tigers.

DISCUSSION

The most significant findings of this study were that 5 of 6 rehabilitated tigers were able to successfully hunt and survive in the wild after spending the majority of their subadult lives in captivity. These animals demonstrated their ability to seek out and subdue wild prey, focusing primarily on large ungulates, in proportions amazingly similar (86% v. 88% of the diet) to their counterparts in the nearby central Sikhote-Alin Mountains. Total consumption rates of rehabilitated tigers were also nearly identical to the tigers from Sikhote-Alin (Figure 3). We believe these similarities are indicators that rehabilitated tigers were quite successful in adapting to and surviving in their relocated landscapes.

Although our sample size of intensively studied tigers was small (n = 6), from spring 2013 through spring 2021, 13 tigers (8 females, 5 males) were released into the recovery region (Rozhnov et al. 2018, 2021; Miquelle et al. 2024). All 13 survived for extended periods of time in the wild (at least for the duration of battery life on their GPS collars), and only one of the tigers (as reported above) came into conflict with humans and had to be removed from the wild. Through this same period, at least 4 females produced 6 litters (≥12 cubs), sired by both wild males (dispersing from the Sikhote-Alin population), and rehabilitated males released as part of this program (Rozhnov et al. 2021; ANO Tiger Annual Reports: https://amur-tiger.ru/en/library?filter=cat-4). Some of these offspring survived and dispersed, adding to the population (Miquelle et al. 2024). Hence, the answer to our first question, "would orphaned tigers, born in the wild but raised in captivity, become sufficiently proficient in hunting wild prey to survive and reproduce in the wild?" appears to be an emphatic yes.

The answer to the second question, "would tigers adequately avoid domestic animals as a source of food?" is more nuanced. The large majority of prey taken were wild, but some dogs and cattle were preyed upon by multiple animals. Apart from predation patterns by one tiger, all domestic prey were killed in forests, meaning that tigers were, for the most part, not moving into villages and fields to prey on domestic livestock. This interpretation is supported by 2 facts: 1) except for the single tiger that was removed after repeated depredations, there were no reports or complaints from local people associated with other tigers; and 2) the proportion of domestic animals taken by reintroduced individuals was low and similar to that of wild tigers in Sikhote-Alin (Figure 2). However, the one male tiger caused considerable mayhem in China, killing domestic dogs, goats, and sheep on multiple occasions. He may have become more conditioned to seek domestic animals while in China, where there were few wild prey alternatives in the areas where he roamed, and where, at least in some instances, people were intentionally putting out dead domestic animals as food for this tiger. Therefore, shortly after he returned to Russia, this tiger was removed from the wild. This individual was raised alone in an enclosure at the rehabilitation center closest to the observation station where humans commonly came and went. His enclosure had the least cover (consisting mostly of tall grasses) and pre-release testing indicated his human avoidance indices were minimally acceptable compared to other captive tigers. This particular enclosure was not used for rehabilitation of any other tigers released into the Pri-Amur. Hence there appear to be multiple factors that could have contributed to this tiger's predilection for domestic prey. Such situations underscore the importance of having experienced teams capable of quickly and efficiently managing conflicts and removing problem animals when necessary (Goodrich et al. 2011).

Pri-Amur tigers killed smaller prey at a higher rate than Sikhote-Alin tigers (Figure 3), a pattern driven potentially by several factors. At the time of release in the Pri-Amur region, wild boar were abundant, including many young. Wild boar are highly preferred prey in the central Sikhote-Alin, possibly because they are easier to stalk and kill than other large mammals (Miquelle et al. 2010, Yudakov and Nikolaev 2012). It is not surprising that younger, smaller, and inexperienced rehabilitated tigers selected smaller, more vulnerable prey. Although Sikhote-Alin tigers also generally selected smaller-sized wild boar in the exact same proportions as Pri-Amur tigers, small wild boar represented a greater proportion of the diet of Pri-Amur tigers, resulting in an overall smaller average prey size. We suspect that average prey size likely increases as tigers increase in size and become more experienced, especially for females needing to feed multiple cubs (Miller et al. 2014, Petrunenko et al. 2020). Even though prey size was smaller, rehabilitated tigers made up for that difference by increasing their kill rate. Ultimately, the differences between kill rate and kill size balanced out, resulting in consumption rates nearly identical to those of tigers studied in the central Sikhote-Alin (Figure 3C).

This study also provided insights into the relationships of tigers to other large carnivores. As with tigers in the central Sikhote-Alin, rehabilitated tigers were not averse to killing and eating other large predators, although such predations were rare in both areas. Both groups of tigers preyed on both species of bears they encountered. Generally, however, tigers preyed on smaller individuals, likely exploiting opportunities with lower risks. In addition to bears, an inverse relationship has been documented between the abundance of tigers and wolves, with wolves becoming functionally absent where tigers are abundant (Gromov and Matyushkin 1974, Miquelle et al. 2005*b*, Salkina and Eremin 2017). However, the mechanism by which this happens is unclear, as wolves are generally rare in the Sikhote-Alin Mountains and there is little evidence documenting predation on wolves by tigers in the region (Miquelle 1966, Makovkin 1999). Release of rehabilitated tigers into Pri-Amur, where wolves were common, quickly resulted in several cases of predation on wolves. These results provide evidence that direct competition, perhaps in association with avoidance by wolves, is responsible for the inverse relationship between tiger and wolf population dynamics, and that tigers are one of the few species within the global range of wolves that can outcompete and drive wolves to functional extirpation in ecosystems where they co-exist.

CONSERVATION IMPLICATIONS

We provide some of the first evidence that orphaned tiger cubs can be successfully rehabilitated and returned to former parts of the species' range. The success of rehabilitated tigers in the Pri-Amur region is particularly important because reintroductions of top predators have been approached cautiously, often with recommendations to consider options other than reintroduction (Hayward and Somers 2009) because of the obvious concerns about dangerous carnivores and conflict. However, if natural, fully functional, and biologically diverse ecosystems are to be restored, the presence of top carnivores will be a key indicator of success. Across Asia there are over 700,000 km^2 of potentially suitable habitat where tigers could possibly be reintroduced (Sanderson et al. 2023), pending mitigations to address reasons for their original extinction from those patches (International Union for Conservation of Nature 2013), indicating opportunities to return tigers and help restore ecological integrity across much of the region.

Wild adult individuals who have already demonstrated their ability to survive in the wild are the ideal translocation candidates for reintroductions (Becker et al. 2022). Yet our data indicate that where adult wild translocation candidates may not be an option, release of captive animals may be feasible if raised in the absence of humans and given opportunity to learn how to hunt appropriate wild prey. Even though orphaned tiger cubs were kept in conditions that were not an exact replication of those tigers would face when released back into the wild, they were sufficient to ensure the majority of tigers successfully made the transition, were able to secure native, wild prey, and even successfully reproduce and raise young. Our results imply that, if human contact is kept to a minimum, innate avoidance of humans is retained in tigers even after extensive periods of time in captivity. Yachmennikova et al. (2018) suggest that socialization and reactions to strangers are formulated during the developmental process of tiger cubs, indicating that perhaps even tigers born in captivity but kept separate from humans would also retain that innate tendency to avoid humans. If this were true, carefully managed tiger populations at accredited zoos could become sources for reintroductions. Use of captive-born individuals are experiments yet to be conducted (at least for tigers), but the experiences of rehabilitating young wild cubs and releasing them into the wild in Russia provides a potential framework for reintroductions of other big cats across the globe where adult wild translocation candidates are not available.

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CONFLICT OF INTEREST STATEMENT

All authors have declared no conflict of interest associated with this manuscript.

ETHICS STATEMENT

Capture and handling of all tigers followed guidelines of the American Society of Mammalogists (Sikes et al. 2011), and protocols were approved by the Wildlife Conservation Society Global Health unit.

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SUPPORTING INFORMATION

Additional supporting material may be found in the online version of this article at the publisher's website, including a Russian language version of this article.

Tables and Figures

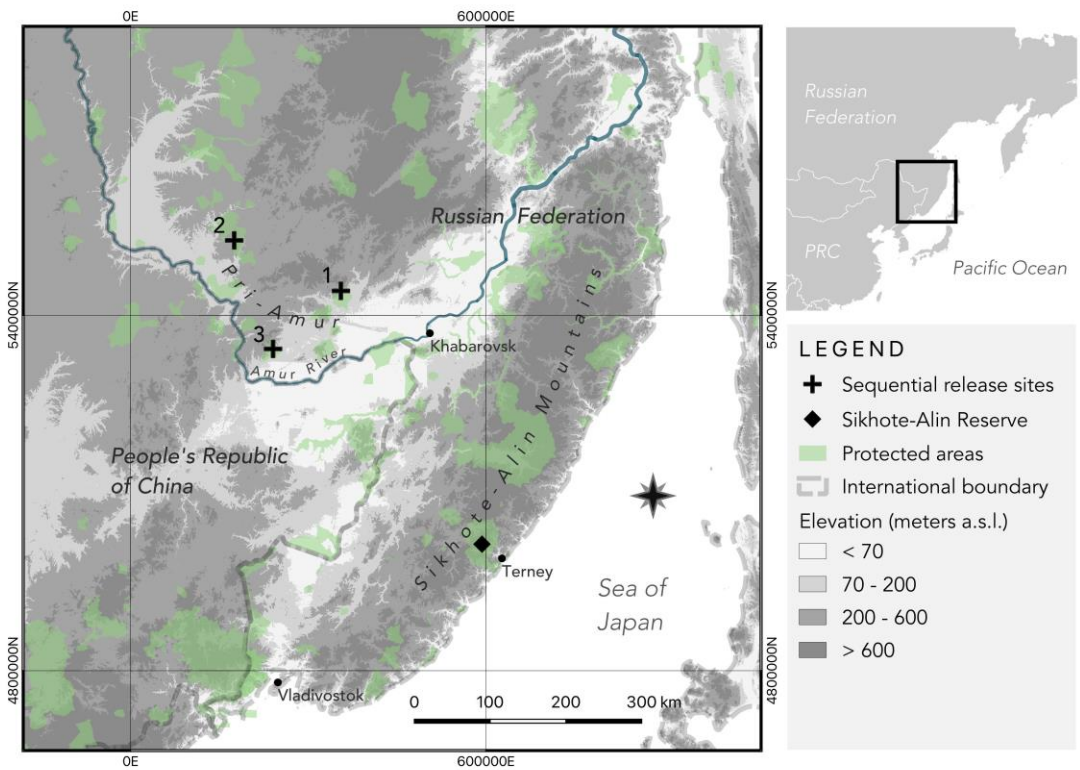

Figure 1. Study areas, sequential release sites in 2013–2014 (listed as 1, 2, 3) for rehabilitated Amur tigers, and key protected areas in Pri-Amur region and Sikhote-Alin Mountains of the Russian Far East. Food habits and kill data of tigers in the central

Sikhote-Alin region, referenced in-text, came from tigers in and around Sikhote-Alin Zapovednik.

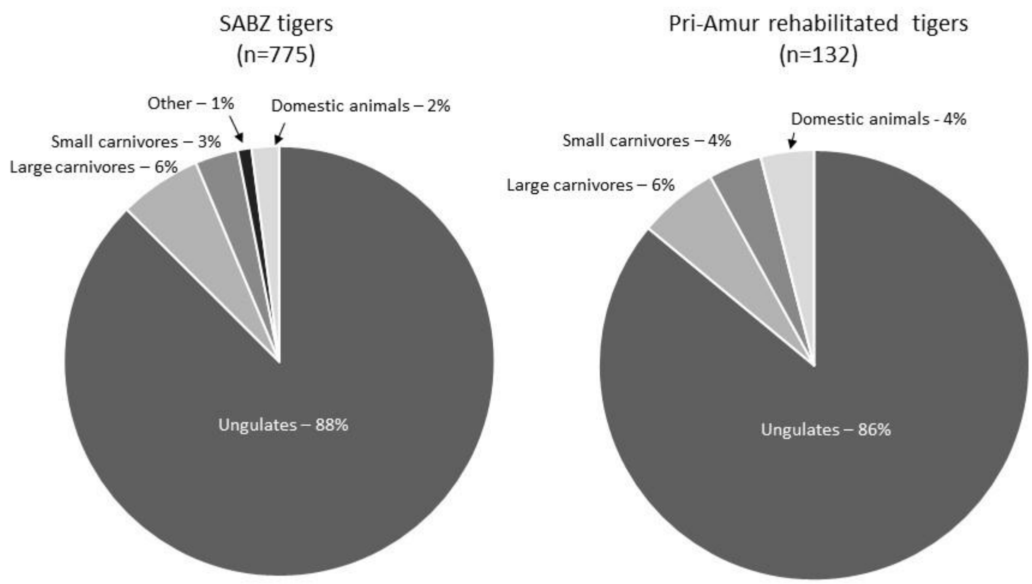

Figure 2. Diet composition of Amur tigers in and around Sikhote-Alin Reserve (SABZ) from 1992-2012 and tigers released into the Pri-Amur region of the Russian Far East (2013-2016) based on evidence at kill sites of collared individuals (sample size in parentheses). We aggregated diet composition as proportion of kills of wild ungulates, large carnivores, small carnivores, other wild prey, and domestic animals (dogs, cows, horses).

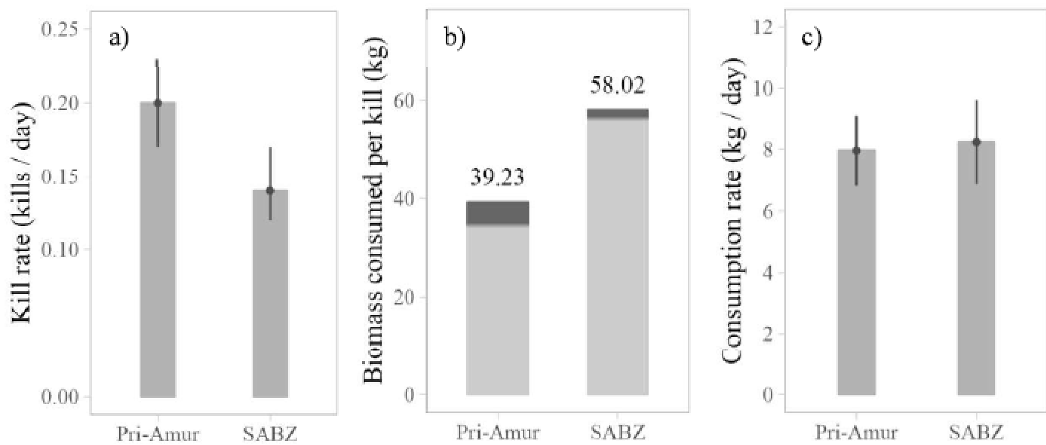

Figure 3. Comparison of A) kill rates, B) average biomass consumed per tiger per kill, and C) consumption rates for Amur tigers released into the Pri-Amur region after rehabilitation (Pri-Amur; 2013–2016), and tigers captured in the Sikhote-Alin Biosphere Zapovednik (SABZ; 1992–2012) in the Russian Far East. Uncertainty in kill rates and consumption rates are presented as 95% confidence intervals. In frame B, each bar is shaded by prey type: light gray = wild ungulates; dark gray = wild carnivores; medium gray = all other prey.

Table 1. Kill composition of rehabilitated Amur tigers released into the Pri-Amur region of Russia studied from 2013-2016, and tigers monitored in and around Sikhote-Alin Reserve (SABZ) in the central Sikhote-Alin Mountains (1992-2012).

	Prey species		% of kills found	
Prey category	Common name	Scientific name	Pri-Amur rehabilitate	SABZ tigers

			d tigers (*n* = 132)	(*n* = 775)
Wild ungulates	Red deer	*Cervus elaphus*	3.0	43.2
	Wild boar	*Sus scrofa*	55.3	25.0
	Sika deer	*Cervus nippon*		9.0
	Roe deer	*Capreolus pygargus*	23.5	9.2
	Moose	*Alces alces*	3.8	0.1
	Musk deer	*Moschus moschiferus*		0.5
	Amur goral	*Nemorhaedus caudatus*		0.4
Large carnivores	Brown bear	*Ursus arctos*	1.5	4.9
	Asiatic black bear	*Ursus thibetanus*	0.8	0.9
	Wolf	*Canis lupus*	3.8	
	Tiger	*Panthera tigris*		0.4
Small carnivores	Badger	*Meles leucurus*	3.8	2.2
	Raccoon dog	*Nyctereutes procyonoides*	0.8	0.9
	Red Fox	*Vulpes vulpes*		0.1
Other	Spotted seal	*Phoca largha*		0.9
	Ural owl	*Strix uralensis*		0.1
Domestic	Domestic dog	*Canis lupus familiaris*	2.3	1.4
	Cattle	*Bos taurus*	1.5	0.5
	Horse	*Equus ferus caballus*		0.1

Total				100	100

Table 2. The top 8 multiple logistic regression models predicting Amur tiger kill sites in Sikhote-Alin Biosphere Reserve (SABZ; 2010-2011) and the Pri-Amur region (2013-2016) in the Russian Far East. Model selection was based on Akaike's Information Criterion for small sample size (ΔAIC_c), which considers number of parameters (K).

Site	Model description[a]	K	Log likelihood	ΔAIC_c	AIC weights
SABZ	Days + fidelity + hours + MD	5	-147.292	0.00	0.299
	Avgdist + days + fidelity + hours + MD	6	-147.209	1.90	0.116
	Days + fidelity + hours + MD + radius	6	-147.268	2.02	0.109
	Days + fidelity + hours	4	-149.607	2.57	0.083
	Fidelity + hours + MD	4	-149.828	3.01	0.066
	Avgdist + days + fidelity + hours + MD + radius	7	-146.881	3.32	0.057
	Fidelity + hours	3	-151.005	3.33	0.057
	Avgdist + days + fidelity + hours	5	-149.521	4.46	0.032
Pri-Amur	Avgdist + hours + MD	4	- 126.035	0.00	0.172
	Avgdist + days + hours + MD	5	- 125.479	0.96	0.106
	Hours + MD	3	- 127.668	1.21	0.094

Avgdist + fidelity + hours + MD	5	- 125.945	1.89	0.067
Avgdist + hours + MD + radius	5	- 125.947	1.89	0.067
Days + hours + MD	4	-127.005	1.94	0.065
Hours + MD + radius	4	-127.396	2.72	0.044
Fidelity + hours + MD	4	-127.407	2.74	0.044

[a] Variables included the number of 24-hour periods between the first and last location of a cluster (days), the proportion of locations for the duration of a cluster that were within the cluster (fidelity), number of hours between the first and last location of a cluster (hours), a binary variable indicating whether a tiger spent more or less than 24-hours at the cluster (multiday [MD]), the average distance of all locations within the cluster to its center (avgdist), and the distance between the center of a cluster and its farthest point (radius).