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To cite this version:

Dawei Wang, James Smith, Francesco Accatino, Jianping Ge, Tianming Wang. Addressing the impact of canine distemper spreading on an isolated tiger population in northeast Asia. Integrative Zoology, 2023, 15 p. 10.1111/1749-4877.12712 . hal-04055682

Addressing the impact of canine distemper spreading on an isolated tiger population in northeast Asia

Running title: PVA of Amur tiger population

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Open Research statement: Simulated data is available in Science Data Bank at https://doi.org/10.57760/sciencedb.02627.

Acknowledgments: This work was supported by the National Natural Science Foundation of China (31971539), the National Science and Technology Basic Resources Survey Program of China (2019FY101700) and a scholarship from the China Scholarship Council (202106040062).

Author contributions: T.W. and D.W. conceived the ideas and designed the study; D.W. involved in the development of the PVA model, writing–original draft, and visualization. J.L.D.S., F.A. and J.G advised on the analyses. All authors contributed critically to the drafts, and gave final approval for publication.

Conflict of interest statement: The authors declare no conflict of interest.

Abstract

The continuation of the isolated Amur tiger (*Panthera tigris altaica*) population living on the China-Russia border is facing serious challenges due to factors such as its small size (including 38 individuals) and canine distemper virus (CDV). To assess options to reduce the impact of these negative factors, we use a population viability analysis (PVA) metamodel, which consists of a traditional individual-based demographic model linked to an epidemiological model, to assess options for controlling the impact of negative factors through domestic dog management in protected areas, increasing connectivity to the neighboring large population (including more than 400 individuals) and habitat expansion. Without intervention, under inbreeding depression of 3.14, 6.29 and 12.26 lethal equivalents, our metamodel predicted the extinction within 100 years is 64.4%, 90.6% and 99.8%, respectively. In addition, the simulation results showed that dog management or habitat expansion independently will not ensure tiger population viability for the next 100 years, and connectivity to the neighboring population would only keep the population size from rapidly declining. However, when the above three conservation scenarios are combined, even at the highest level of 12.26 lethal equivalents inbreeding depression, population size will not decline, the probability of extinction will be $< 5.8\%$. Our findings highlight that protecting the Amur tiger necessitates a multifaceted synergistic effort. Our key management recommendations for this population underline the importance of reducing CDV threats and expanding tiger occupancy to its former range in China, but re-establishing habitat connectivity to the neighboring population is an important long-term objective.

Keywords: Amur tiger; Canine distemper virus; Habitat connectivity; Metamodel; Population viability analysis (PVA)

1 INTRODUCTION

The tiger (*Panthera tigris*), a flagship species in Asia, has declined to fewer than 5,000 individuals remaining in less than 7% of the surface of its historical range (Joshi *et al.* 2016; Jhala *et al.* 2021). Among the five extant subspecies, the Amur or Siberian tiger (*P. t. altaica*) is the northernmost (Wang *et al.* 2018). It suffered a severe decline in the mid-20th century, and currently has a low level of genetic diversity (Henry *et al.* 2009; Dou *et al.* 2016). Fewer than 550 wild Amur tigers exist; they are distributed in two populations separated by urban conglomerates and highways (Miquelle *et al.* 2007; Wang *et al.* 2018). The larger population is spread widely in the Sikhote-Alin mountains, Russia, and the smaller isolated Changbai-Primorye population (< 40 tigers) is restricted to the China-Russia border (Hebblewhite *et al.* 2014; Feng *et al.* 2017). The Changbai-Primorye population represents the main source for recovery of the Amur tiger in much of its former range in northeast China (Miquelle *et al.* 2010; Wang *et al.* 2016; Qi *et al.* 2021).

Unfortunately, this population is currently facing multiple threats, including insufficient prey resources (Wang *et al.* 2018), fragmentation and degradation of habitat (Hebblewhite *et al.* 2014; Wang *et al.* 2016), poaching (Robinson *et al.* 2015), and inbreeding depression (Henry *et al.* 2009; Ning *et al.* 2021). Furthermore, recent studies have shown that tiger populations are facing an emerging threat from canine distemper virus (CDV). CDV is a nearly globally distributed RNA virus (Deem *et al.* 2000; Adhikari *et al.* 2020) that has caused significant decline in carnivore populations such as Serengeti lions (*P. leo*) (Roelke-Parker *et al.* 1996; Weckworth *et al.* 2020) and Ethiopian wolves (*Canis simensis*) (Gordon *et al.* 2015). As early as 2000, CDV was reported in the Sikhote-Alin Amur tiger population (Quigley *et al.* 2010; Gilbert *et al.* 2015), and CDV was a factor responsible for a rapid decline of the Sikhote-Alin population (Miquelle *et al.* 2015). Although not yet detected in the Changbai-Primorye population, studies have shown that CDV has been spreading within sympatric population of Amur leopard (*P. pardus orientalis*) (Sulikhan *et al.* 2018). The consequences of CDV spread to Changbai-Primorye Amur tiger population could be devastating. The multi-host nature of CDV poses a great threat to felid populations that coexist with other hosts. For the Sikhote-Alin and Changbai-Primorye tiger populations, free roaming domestic dogs that are occasionally killed by tigers (Sugimoto *et al.* 2016; Dou *et al.* 2019) constitutes a potential reservoir of infection for tigers (Craft *et al.* 2009), who provide 3-6% of the biomass consumed of tigers (Gu *et al.* 2018; Dou *et al.* 2019). Few studies have assessed the impact of CDV on a critically small endangered tiger population.

Currently, China and Russia are cooperating to conserve this population through joint monitoring (Feng *et al.* 2017). Additionally, in 2016, the Chinese government established a National Park, that expanded three Amur tiger and leopard reserves in China to create a ~15,000 km^2 Northeast Tiger Leopard National Park. This expansion is linked to the Land of Leopard Reserve, Russia, which has formed an 18,000 km^2 landscape for large felids. However, human development has effectively blocked continuous genetic exchange between Changbai-Primorye and the Sikhote-Alin population, increasing the risk of inbreeding depression in the Changbai-Primorye population (Henry *et al.* 2009; Sorokin *et al.* 2016).

Given the isolation and low genetic diversity of this population and the specific threats of CDV, a population viability analysis (PVA) is urgently needed for the Changbai-Primorye tiger population. Previous PVAs of the Amur tiger assessed the impact of habitat connectivity and fragmentation (Carroll & Miquelle 2006; Tian *et al.* 2011), and the influence of CDV on the larger Sikhote-Alin population (Gilbert *et al.* 2020). However, when CDV and other wildlife diseases are incorporated in PVA models they are usually treated as a general random effect and operate at the same time scale as the PVA. Epidemic disease such as CDV have dynamics that are often strongly related to the specific host populations and they operate at a rapid temporal scale not captured in a typical PVA analysis using an annual time step (Smith *et al.* 2009; Shoemaker *et al.*

2014). Therefore, in this study, we modeled the viability of the Changbai-Primorye tiger population combining a traditional PVA (Lacy & Miller 2020) with a separate CDV epidemiological model (Lacy *et al.* 2020). This metamodel approach is commonly used to simulate the spread of epidemic diseases within wild populations (Bradshaw *et al.* 2012).

Here, we assess the probability of the persistence of the Changbai-Primorye population for the next 100 years. We (i) use a metamodel modelling approach to determine the impact of CDV infection, lack of connectivity and restricted habitat which threaten the long-term viability of this population and (ii) assess the most effective combinations of management strategies that increase CDV infection control, expand habitat into its former range in China and establish population connectivity with the larger Sikhote-Alin population. Our results provide guidance for conservation policies to enhance the viability of the Changbai-Primorye population.

2 MATERIALS AND METHODS

2.1 Study area

The smaller Changbai-Primorye tiger population occurs in the Changbai Mountains in the Jilin and Heilongjiang provinces of China and in the Land of Leopards National Park in southwestern Primorye Province (Figure 1). The Changbai Mountains are one of the highest priority Conservation Areas in China. This landscape consists of a large network of habitat patches, which are connected with the Land of Leopards National Park in Russia (Hebblewhite *et al.* 2012). In 2015, based on long-term monitoring, we estimated the Changbai-Primorye population contained at least 38 tigers (13 adult females, 10 adult males, 3 unidentified adults, and 12 sub-adults/cubs) occupying 9,000 km^2 along the China-Russia border (Feng *et al.* 2017). The elevations of the rugged landscape ranges from 5m to 1477 m and has a temperate continental monsoon climate that supports a temperate coniferous broad-leaved mixed forest. Due to long-term deforestation, many low-elevation forests in these areas have been transformed into secondary deciduous forests (Wang *et al.* 2016). The main prey species of Amur tigers in this area are wild boar (*Sus scrofa*), sika deer (*Cervus nippon*), Siberian roe deer (*Capreolus pygargus*), and domesticated species, such as cows and dogs (Kerley *et al.* 2015). The area has been subjected to cattle grazing, ginseng planting, frog farming, and edible fern collection for decades, particularly on the Chinese side (Feng *et al.* 2021).

2.2 Modelling overview

We developed a metamodel using two spatially implicit submodels to assess the extinction risk of the tiger population (Figure 2): an age- and sex-structured, individual-based stochastic demographic model based on Vortex software (version 10.5.0) (Lacy & Miller 2020) and an individual-based epidemiological model that simulates epizootics such as CDV built with Outbreak software (version 2.11.0) (Lacy *et al.* 2020). The two submodels were connected by the Metamodel Manager (version 1.0.6) (Pollak & Lacy 2020), which transfers information back and forth between submodels as “open data” that are updated by each before being passed on. All scenarios were projected for 100 years, with 500 model runs, each one with a specific draw of parameter values from its probability distributions or specified; the results of population size and genetic diversity were averaged across the runs. The population survival probability was calculated as the percentage of simulations ending with population survival.

2.2.1 Tiger demographic model

We used Vortex to build a demographic model for the tiger population with one year as a time step. Cubs and juveniles do not maintain their own territories (Tian *et al.* 2011) and male territories overlap with those of 1-3 females, while the overlap between females is relatively low (Hernandez-Blanco *et al.* 2015; Xiao *et al.* 2016). Thus, in this study, the habitat carrying capacity was measured in terms of female tiger home ranges; the initial habitat of 9,000 km^2 can accommodate approximately 23 females with an average home range of approximately 400 km^2 (Hernandez-Blanco *et al.* 2015). The gestation period of the Amur tiger is 95-100 days, and the time of caring for the cubs is approximately 18.8 months (Kerley *et al.* 2003). So, we used 2 years both for time that young were dependent on their mother and the interbirth interval. If a female tiger died, all of her currently dependent offspring also died. For the mortality rates of the Amur tiger, we refer to mortality data from 1992 to 2012 in the Sikhote-Alin Mountains, Russia (Robinson *et al.* 2015). Poaching has been a severe threat to wild tiger survival (Kenney et al. 1995), but because of the Changbai-Primorye population’s strong protection and transboundary cooperation, we used a mortality rate of subadults and adults as the sum of the natural mortality rate (5.1%) and 50% of the Sikhote-Alin population’s poaching death rate (10.3%) (Robinson *et al.* 2015). In addition, inbreeding depression has been confirmed to exist in wild tiger populations (Smith & Mcdougal 1991), and the Amur tiger population in China has reached a moderate level of inbreeding (Ning *et al.* 2021), but accurate lethal equivalents to measure the severity of inbreeding depression have not been available. So we conservatively set the base line lethal equivalents to 3.14 (Ralls *et al.* 1988) and then examine the impact of higher lethal equivalents rated (6.29 and 12.26) more recently estimated by O’Grady et al. (2006). Other model parameters are from previously reported tiger studies (see Table 1, Appendix S1 for the details and main parameter input).

2.2.2 Epidemiological modelling

We developed an individual-based epidemiological model with one day as a time step using Outbreak, to simulate CDV transmission in the tiger population in the low-risk outbreak year. The model incorporates complex processes such as interindividual transmission, pathogen environmental transmission, incubation period, infection period and infection outcome. In the model, there are two main ways for tigers to become infected with CDV: (i) contact with environmental disease sources, such as predation on small and medium-sized wild predators and dogs carrying the virus or (ii) intraspecific transmission through social contact. According to Gilbert et al. (2014), the probability of CDV infection of Amur tigers by feeding on infected domestic dogs or small carnivores is 1.4%, and the average daily infection probability is 0.003836% (Appendix S2: Table S1). We set the probability of infection in the interaction process as 1.4% of the cumulative prevalence rate of CDV within one year (see Table 2, Appendix S2 for the details and main parameter input). Furthermore, to simulate CDV's cyclical high-risk prevalence (Roscoe 1993), we applied 5 years of cyclically high infection risk to the model (Gilbert *et al.* 2014). In the high risk outbreak year, we set an additional mortality rate of 11.48% in the "catastrophes" module of Vortex (Table 1).

2.3 Sensitivity analysis

We developed a set of scenarios to assess how uncertainty about parameter values affect metamodel outcomes. We tested 9 key parameters in the sensitivity analysis. For lethal equivalents (LEs), in addition to a base line rate of 3.14, we examined values of 6.29 and 12.26 estimated through meta-analyses of multiple wild species (O'Grady et al. 2006; Kenney et al. 2014). To evaluate the impact of temporal high-risk cycles of CDV infection (CCI) we used cycles of 3, 7 and no high infection cycle. For poaching intensity (PI) we tested poaching mortality rates of 0 and 10.3% as reported by Robinson et al. (2015) (see Appendix S1 for the details). For the other 6 parameters, mortality rate after CDV infection (MCI), successfully breeding female proportion (BFP), infant-cub (0-1 year old) mortality rate (IMR), adult (>3 years old) female mortality rate (FMR), adult (>3 years old) male mortality rate (MMR), and carrying capacity (K), we increased or decreased the baseline value by 40% (He *et al.* 2020). A total of 19 scenarios were created for this analysis. We varied each key parameter while holding all other parameters to baseline values. The outputs of each sensitive scenario were compared to the baseline scenario: mean stochastic population growth rate (R), mean population number at the 100th year (N), population genetic diversity at the 100th year (GD), probability of extinction (PE), and mean time of extinction (TE). The sensitivity index (Pulliam *et al.* 1992) of the mean stochastic population growth rate for each simulation parameter was calculated as follows:

$$S_R = | (\Delta R / R) / (\Delta P / P) |$$

$\Delta R/R$ represents the variable ratio of the mean stochastic population growth rate over 100 years; $\Delta P/P$ represents the variable ratio of the parameters. The sensitivity index is proportional to the influence of the parameters on the output of the model.

2.4 Tests of alternative management actions

Based on the recent threats faced by the Amur tiger, we developed three scenarios to assess how different management actions and their combinations affect the probability of extinction of the Changbai-Primorye population (Appendix S4: Table S1 and Appendix S3).

Scenario A: CDV control

For Scenario A, we reduced the risk of CDV infection in Amur tigers by managing free-ranging domestic dogs (e.g., vaccination, hereafter referred to as “dog control”). The probability of the tiger being infected with CDV due to predation on dogs was reduced to 0, the probability of CDV transmission between individuals in low-risk years was 0.99%, the daily average pathogenic environmental infection probability was 0.002712%, and the mortality rate of CDV infection in high-risk years was 83.8%. These parameters were derived from published studies on the influence of CDV on Amur tigers (Gilbert *et al.* 2014, 2015).

Scenario B: habitat connectivity

For Scenario B, we constructed a larger population (the initial population contains 454 individuals and the habitat can hold 502 adult female tigers) in the model, based on the population characteristics of the neighboring larger Sikhote-Alin population. Then we established habitat connectivity between large and small populations by exchanging individuals between populations. According to the research of Henry et al. (2009), before the complete separation of the two populations, the probability of individuals in the large population dispersing to the small population is 0.22%, and the probability of individuals in the small population dispersing to the large population is 1.3%. In the model we use this pair of dispersion rates.

Scenario C: habitat expansion

Scenario C was divided into two options. For the first option scenario C45, tiger habitat increased to 18,000 km^2 within 20 years, which could accommodate 45 female tigers, based on the plan of Wang *et al.* (2018) that designated protected habitat becomes occupied. For the second option scenario C100, tiger habitat increased to 40,000 km^2 in 30 years and can accommodate 100 female tigers, based on Hebblewhite et al.'s (2012) estimate of potential recoverable core habitat in China (see Appendix S3).

2.5 Inbreeding depression

To avoid underestimating the degree of inbreeding depression in wildlife populations, in addition to the inbreeding depression test for 3.14LEs, we also examined the impact of 6.29 LEs based on Kenney et al. (2014) and 12.26 LEs based on O'Grady et al. (2006), to assess population trends under different cases of inbreeding depression. We set the absence of any management alternatives as the baseline for each inbreeding depression scenario. In the simulation of 3.14 LEs, the inbreeding only affected the first-year survival. In the simulation of 6.29 LEs, 3.94 LEs were used to impact fecundity and 2.35 LEs to reduce first-year survival. In the simulation of 12.26 LEs, we added 5.97 LEs for altering survival from age 1 to sexual maturity based on 6.29 LEs.

3 RESULTS

3.1 Baseline scenario

The baseline scenario (no management actions) predicted that under inbreeding depression of 3.14 LEs, the small population would decrease at a mean rate of 0.018 per year, and would have a 64.4% extinction probability within 100 years. The mean time of extinction was 66 years, the mean population size was 7 individuals and the population genetic diversity would decline to 57.0% of its original level (Table 3).

3.2 Sensitivity analysis

The results showed that the three parameters with the highest sensitivity indices were BFP, MCI and IMR (Table 3, Figure S1 in Appendix S4). The effect of different parameter variations on the simulation were as follows: for LEs of 6.29 and 12.26, the extinction probability at 100 years was 90.6% and 99.8%, respectively and mean population size declined to 1 and 0, respectively (Table 3). For CCI, the longer the interval between high infection rates, the slower the population declines. However, when the infectious cycle increased to 7 years, the population extinction probability was still high (43%), but when cycle of CDV high infection risk was removed, the probability of extinction dropped to 0, and the population slowly grew from an initial size of 38 to 58 individuals after 100 years. For PI, when the mortality caused by poaching was set at 0% and 10.3%, the extinction probability was 1.8% and 99.8%, respectively. When poaching was fully eradicated, the population grew slowly, reaching a size of 56 after 100 years. The population exhibited a growing trend when MCI, IMR, and FMR were reduced by 40% and BFP was increased by 40%. For MMR and K, their increase or decrease had little influence on the population (Table 3).

3.2 Tests of alternative management actions

Just reducing domestic dogs (scenario A), even in the mildest inbreeding depression category (3.14 LEs), resulted in a negative growth rate (-0.006), the population extinction probability was 40.6%, and the population size declined to 16 within the 100 years. In the other two more severe inbreeding depression cases, the population is at a high risk of extinction, with extinction probability above 75% (Figure 3 and Table S2 in Appendix S4).

Increasing habitat connectivity (scenario B), with inbreeding depression at 3.14 and 6.29 LEs, resulted in a mean stochastic growth rate was 0.013 and 0.008, the mean population genetic diversity all declined to 89%, the population size reached 43 and 37, and the extinction probability within 100 years dropped to 1.4% and 4.2%, respectively. However, in the case of 12.26 LEs, the mean stochastic growth rate was 0 and the extinction probability was 14.4% (Figure 3 and Table S2 in Appendix S4).

Expanding the tiger’s range (scenario C) alone was inadequate. For both schemes (C45, C100), the simulation results were essentially the same as the baseline under the different inbreeding depression, except for a slight difference in population size in the 100th year. The population remained at high risk of extinction (Figure 3 and Table S2 in Appendix S4).

In summary, as the value of LEs increases, the benefits of implementing just one of the scenarios was largely ineffective. Habitat connectivity provided the biggest benefit. Implementing both habitat expansion and reducing the number of dogs in the forest have smaller benefits, but increasing habitat is the least beneficial (Figure 3). We chose the expansion scheme of 45 females (C45) as the representative of the habitat expansion scenario and simulated four combinations of the three scenarios overlapping each other. We found that the benefits of the four combinations were much higher than those of single management action (Appendix S4: Table S2, Table S3), regardless of the LEs (Figure 4). In the combination of scenario A and C at three levels of LEs, the population size reached 44, 13 and 0 within the 100th year, the genetic diversity was 71.3%, 66.7%, 0.00%, the mean stochastic growth rate was -0.002, -0.018, and -0.049, and the population extinction probability was 26.4%, 57.8%, and 99.8%, respectively; in the combination of scenarios B and C with the 3 possible levels of LEs, the population size was 73, 56, and 11, and the genetic diversity was 90.5%, 89.7%, and 88.4%, respectively, the mean stochastic growth rate was 0.008, 0.003, and -0.016, and the extinction probability was 2.2%, 3.4%, and 44.2% within 100 years, respectively; in the combination of scenario A and B of three levels LE, the population size was 59, 56, 32, the genetic diversity in the 100th year was 93.3%, 93.3%, and 90.0%, and the mean stochastic growth rate was 0.030, 0.024, and 0.004, respectively. And there was no risk of population extinction within 100 years in the 3.14 and 6.29 LEs but the extinction probability with 12.26 LEs was 5.6%; when the three actions were combined, the population size was 110, 97, 41, genetic diversity in the 100th year was 93.8%, 93.8%, 91.1%, and the mean stochastic growth rate was 0.021, 0.016, and 0.005, respectively. There was no risk of extinction in the 3.14 and 6.29 LEs cases, but the extinction probability with 12.26 LEs was 5.6% (Appendix S4: Table S3).

4 DISCUSSIONS

By incorporating a metamodel, we were better able to capture the potential dynamics of the rapid spread of CDV within the Changbai-Primorye tiger population and thus obtain a more realistic prediction of the impact of CDV on tigers. Compared with previous PVA tiger studies (Carroll & Miquelle 2006; Tian *et al.* 2011), the contributions of our study are as follows: (i) the metamodel allowed us to incorporate the detailed, rapid dynamics of CDV into a tiger PVA, (ii) we incorporated recent estimates of inbreeding depression that may be more realistic than those used in previous models, and (iii) under these different levels of inbreeding depression and a realistic model of CDV, we were able to explore management options for recovery of the Changbai-Primorye tiger population. Through the simulation of different management measures and their combinations, our results clearly show the importance of habitat connectivity.

4.1 Insights from sensitivity assessment

Our results highlighted that with an outbreak of CDV, this population may require a combination of management strategies to insure its persistence. The extinction probability was greater than 60% under all realistic baseline estimations of lethal equivalents without any intervention. Sensitivity analysis examined the impact of variation in key demographic parameters on the model output results. Variation in the proportion of breeding females was the most sensitive parameter in our sensitivity analysis but based on observations in Nepal and Thailand (James L.D. Smith pers. comm.) there is actually little variation in proportion of females that get pregnant. In contrast, variation in female and infant-juvenile mortality does occur in wild populations and can have a strong negative impact of recruitment. In tigers and other large felids, female survival is a major determinant of population viability (Kenney et al. 2014). This finding is consistent with PVA studies of other mammals such as the fennec fox (*Vulpes zerda*), the Asian elephant (*Elephas maximus*) (He *et al.* 2020; Franklin *et al.* 2021). Therefore, it is critical to ensure female tigers have good breeding habitat and low human-caused mortality to help increase their survival rates (Miquelle *et al.* 2015). Sensitivity analysis also highlighted that poaching intensity, cycles of CDV high infection risk and mortality rate after CDV infection all had critical impacts on the probability of extinction. Without the threat of poaching and CDV, the current population would most likely remain viable for the next 100 years.

The sensitivity analysis showed that changes in environmental carrying capacity did not reduce the probability of extinction. This could be because the Changbai-Primorye population has been kept below the environmental capacity for long periods of time due to multiple threats (Robinson *et al.* 2015; Wang *et al.* 2018; Ning *et al.* 2021), and the influence of inbreeding depression did not decline with habitat expansion. Even if with a large enough habitat, it is difficult for the population to spread to any additional habitat due to the high extinction risk within the population.

Given the difficulty in estimating rates of inbreeding depression in the wild and recent debate as to the extent to which purging reduces inbreeding depression (Armstrong *et al.* 2021), further research is needed to estimate current levels of inbreeding depression in tigers and other species. Alternatively, we may have over-estimated mortality of adult females in our model and that is restricting recovery. Kenney et al. (2014) estimated a much higher annual rate of adult female survival than we used in our model. Future modeling of this population will benefit from efforts to improve estimation of this parameter through our current intensive camera trapping. Simultaneously, it is critical to monitor CDV in both tigers and domestic species.

4.2 Management interventions

With the newly established the Northeast Tiger and Leopard National Park in China, tigers are now expanding their range into northeast China. However, the distribution further from the Russian border is still spotty and the number of tigers is low (Wang *et al.* 2016; Qi *et al.* 2021). Most of the habitat expansion in China is by young males. Female tigers and their young are confined to the China-Russia border and breeding habitat is still estimated at < 6,000 km^2 (Wang *et al.* 2018; Qi *et al.* 2021). At this juncture, urgent actions are needed.

Our study revealed that maintaining connectivity among the two populations was essential and a prerequisite for preventing drastic reduction of population. The simulation of different management scenarios showed that habitat connectivity was the only measure that effectively increased growth rates in the tiger population. Moreover, the scenarios combining habitat connectivity performed relatively well in population projections. In contrast, dog control, habitat expansion and this combination resulted in the population reaching its maximum size in less than 40 years and then gradually declining. It is thus clear that gene exchange among populations plays a key role in the recovery and long-term population persistence.

A true barrier now exists due to continuing development along the Razdolnaya River basin, which prevents movements of tigers between the Changbai landscape and the southern Sikhote-Alin landscape; the populations show clear genetic differentiation (Sorokin *et al.* 2016). Furthermore, a recent study reported poor health status for the Changbai-Primorye population as well as 50% of individual relationships were cousins or half-sibs (Ning *et al.* 2021). Miquelle et al. (2015) used least-cost distance analyses to identify a single potential corridor to retain connectivity for the two subpopulations, but no evidence demonstrates that this corridor is actually used by tigers. When habitat connectivity is difficult to achieve, a more immediate, and practical strategy, is translocation of individuals from the Sikhote-Alin population. A similar movement of Texas panthers into the Florida panther population (*P. c. coryi*) resulted in a dramatic population recovery (Johnson *et al.* 2010; Hostetler *et al.* 2013). Similarly, the reintroduction of tigers in Panna, India, resulted in rapid population recovery (Sankar *et al.* 2010).

CDV infection is regarded as the main threat to large felids conservation not only in Asia but also worldwide (Adhikari *et al.* 2020). Domestic dogs are a proven source of CDV for wild animals and transmit the CDV to the tiger population through direct predation by tigers or indirectly through interaction with other wildlife, which can increase the mortality risk of tigers (Gilbert *et al.* 2014; Dou *et al.* 2019). However, currently, domestic dogs have widely invaded into the Amur tiger's habitat (Gilbert *et al.* 2020). According to our camera-trapping data and field surveys, domestic dogs are still entering the parkland and commited wildlife attacks in 2021; on the Chinese side, unvaccinated domestic dogs had a high level of positive antibodies for CDV due to exposure to the disease (37% in 202 domestic dogs serum tests in 2018, unpublished data). Although dog management practices were not the most effective when compared to habitat connectivity, and domestic dogs may not be the only source of CDV infection (Gilbert *et al.* 2020), dog management was the easiest and safest method to achieve among all conservation actions, and when combined with other measures, it can effectively improve population trajectories by increasing the population recovery speed. Given CDV is preventable, strict vaccination of domestic dogs with the commercial attenuated vaccine is needed. To ensure the long-term success of tiger conservation, we suggest that the local government implement policies aimed at gradually controlling dogs, if not completely prohibiting all dogs in the tiger's core range.

Although the establishment of national park has expanded the habitat of Amur tigers, through the monitoring of camera trap data in the past few years, the core range of Amur tigers still stays at the Sino-Russian border and does not spread to China on a large scale. As the results in our simulations show, the expansion of habitat did not significantly increase the population size, especially in the case of severe inbreeding depression. This may be due to the fact that the Amur tiger population face many threats, such as low initial population size, inbreeding depression and CDV, which cause the population size to remain below the carrying capacity for a long time. Even with sufficiently large habitats, it is difficult for tiger population to spread due to the high risk of extinction. The same result was obtained when assessing the extinction risk of tigers in central India (Thatte *et al.* 2018). Although our model did not indicate that habitat expansion alone would reduce the probability of extinction, habitat expansion has several benefits that should not be overlooked. Habitat expansion would increase structurally and spatial diversity of the landscape, which in turn might decrease the spread of CDV. Also shifting from people intensive logging activities to conservation management may reduce the impact of humans and their dogs serving as a vector for CDV. In India, a topographically and vegetatively diverse landscape also reduced the risk of extinction (Thatte *et al.* 2018).

In summary, our findings highlight the critical need for integrated conservation strategies and actions that link wildlife populations, landscape planning, CDV research, and international cooperation while also meeting human development goals. Our modeling of the potential impact of CDV highlights the critical need for integrated conservation strategies that link and expand wildlife populations, institute broad landscape planning, and include continuous surveys of potential CDV outbreaks. Fortunately, transborder cooperation in monitoring and management is already in place.

4.3 Methodological considerations

Metamodelling requires estimating a number of parameters to build each submodel with an acceptable degree of realism, and hence there is a degree of uncertainty associated with their results (Shoemaker *et al.* 2014). However, metamodels can assist managers and policymakers in making decisions for the conservation of endangered populations in an uncertain environment (Reed *et al.* 2002; Lawson *et al.* 2021). Therefore, this analysis provides the relative benefits of various possible actions rather than an absolute and accurate prediction of future population trends. Inbreeding could have an impact on the survival and reproduction of adult tigers, especially in the face of changing environmental conditions (Coltman *et al.* 1999; Fox & Reed 2011), and population connectivity may slightly mitigate inbreeding depression in populations. However, the above two considerations were not included in the model because of the difficulty of accurately estimating the relevant parameters and their limited influence on the overall population trends. In addition, since prey resources are also an important factor affecting tiger population continuation and management and policy decisions operate on short-term projections, it is necessary to construct more complex and shorter-term projections that include prey species in the future.

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630 **Table 1.** Parameters input for the baseline scenario of the tiger population model in Vortex.

Parameter	Baseline value
Lethal equivalents	3.14
Percent due to recessive lethal alleles (%)	50
Breeding system	Polygynous
Age of first offspring (female/male)	3/4
Maximum age of reproduction	15
Maximum lifespan	15
Maximum number of broods per year	1
Maximum number of progenies per brood	6
Share of males at birth (%)	50
Cubs depend on the mother (years)	2
Successfully breeding female proportion (%)	70
Breeding male proportion (%)	70
Litter size (%)	
1 offspring	10
2 offspring	38
3 offspring	38
4 offspring	10
5 offspring	3
6 offspring	1
Mortality of infant-cubs (%)	40 (0-1)
Mortality of juveniles (%)	20 (1-2)
Mortality of subadults (%)	18.368 (2-3)
Mortality of adult females (%)	6.273 (>3)
Mortality of adult males (%)	15.539 (>3)
Initial population size	38
Number of infant-cubs (female/male)	2/2
Number of juveniles (female/male)	2/2
Number of subadults (female/male)	2/2
Number of adults (female/male)	14/12
Carrying capacity (K)	23 (adult females)
Catastrophes (high risk of CDV)	
Frequency (%)	20
Reproduction	1
Survival (%)	88.52

Table 2. Parameters input for the baseline scenario of the canine distemper epidemiological model in Outbreak.

Parameter	Baseline value
Probability that an individual never becomes susceptible (%)	0
Earliest age of susceptibility (days)	15-30
Transmission probability from an infectious mother to a newborn	1
Time for maternally derived immunity to protect an offspring (days)	150-180
Number of individuals that an individual encounters per day	0.03
Transmission probability among individuals during an encounter (%)	1.40
Daily transmission probability from the environment (%)	0.003836
Duration of the incubation period (days)	2-7
Duration of the infectious period (days)	30-60
Probability of recovering and acquiring permanent immunity (%)	60
Mortality rate after CDV infection (%)	40

Table 3. Baseline candidate model results. R(SD): mean (standard deviation) of stochastic population growth rate across all years and iterations; N (SD): mean (standard deviation) of number of tigers at year 100th; GD (SD): initial genetic diversity (heterozygosity) remaining in population at year 100th; PE: probability of extinction, defined as only 1 sex remains at year 100th; TE: mean time of extinction (in years) for all iterations that went extinct within 100 years; SR: The sensitivity index of the mean stochastic population growth rate for each simulation parameter.

Scenario	R (SD)	N (SD)	GD (SD)	PE	TE	S_R
Baseline	-0.018 (0.186)	7(13)	0.570 (0.1700)	0.644	66	
Lethal equivalents (LEs)						0.691
6.29	-0.030 (0.192)	1 (4)	0.549 (0.189)	0.906	63	
12.26	-0.056 (0.191)	0 (0)	0 (0)	0.998	40	
The cycles of CDV high infection risk (CCI)						1.989
NA	0.057 (0.105)	58 (9)	0.738 (0.093)	0.000	-	
3	-0.037 (0.214)	1 (5)	0.493 (0.176)	0.928	55	
7	-0.008 (0.171)	14 (18)	0.585 (0.178)	0.430	70	
Poached intensity (PI)						2.798
0%	0.037 (0.125)	56 (17)	0.758 (0.092)	0.018	62	
100%	-0.064 (0.244)	0 (0)	0 (0)	0.998	36	
Mortality rate after CDV infection (MCI)						3.791
+40%	-0.042 (0.226)	0 (3)	0.454 (0.238)	0.966	51	
-40%	0.013 (0.138)	33 (20)	0.664 (0.147)	0.128	74	
Successfully breeding female proportion (BFP)						5.228
+40%	0.017 (0.151)	39 (23)	0.674 (0.150)	0.116	66	
-40%	-0.059 (0.218)	0 (0)	0 (0)	1.000	40	
Infant-cub (0-1 year old) mortality rate (IMR)						3.743
+40%	-0.043 (0.204)	0 (1)	0.482 (0.284)	0.982	52	
-40%	0.011 (0.163)	33 (24)	0.659 (0.140)	0.202	71	
Adult (>3 years old) female mortality rate (FMR)						3.342
+40%	-0.040 (0.211)	1 (3)	0.412 (0.253)	0.954	53	
-40%	0.009 (0.157)	30 (20)	0.648 (0.150)	0.168	70	
Adult (>3 years old) male mortality rate (MMR)						0.470
+40%	-0.021 (0.194)	5 (10)	0.497 (0.222)	0.732	63	
-40%	-0.014 (0.173)	11(15)	0.614 (0.183)	0.536	68	
Carrying capacity (K)						0.275
+40%	-0.015 (0.176)	14 (21)	0.624 (0.166)	0.526	65	
-40%	-0.019 (0.209)	2 (6)	0.428 (0.223)	0.844	60	

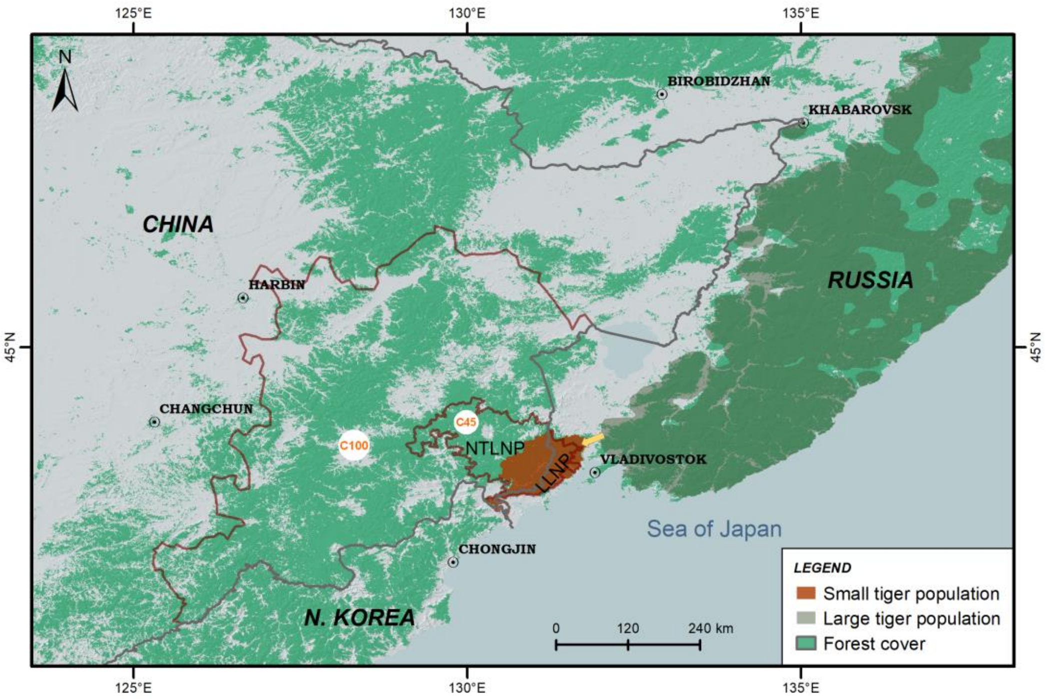

Figure 1. Current range of the Amur tiger in Northeast China and Far East Russia. Small tiger population is areas with confirmed tiger breeding activity within the last 10 years. C100 and C45 indicate two habitat expansion schemes (see method for details). NTLNP and LLNP is the Northeast Tiger and Leopard National Park of China and the Land of Leopard National Park of Russia, respectively. Yellow arrow represents potential important ecological corridors for tigers between small and large populations.

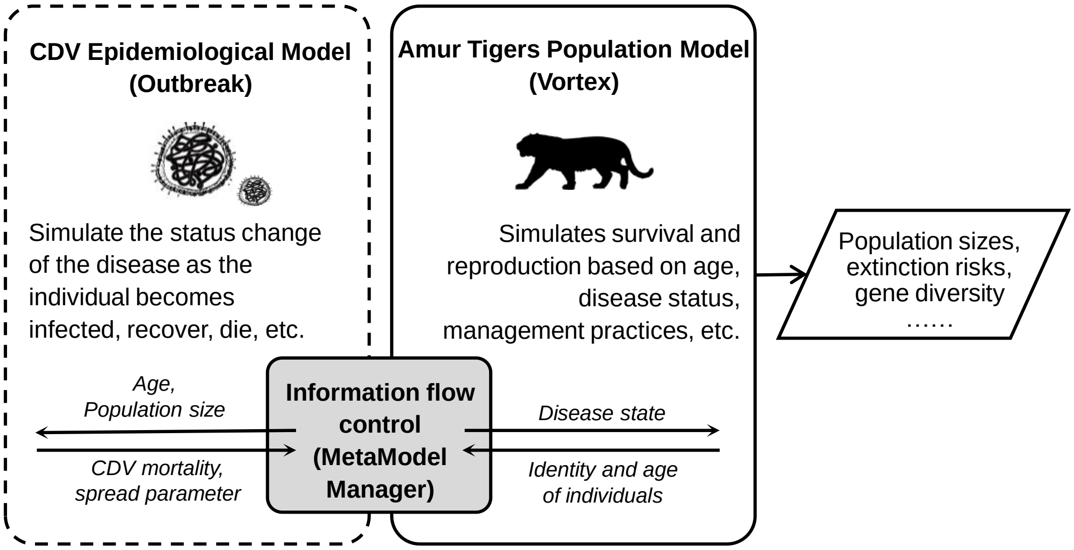

Figure 2. Schematic flowchart of the Amur tiger-CDV metamodel structure used for this analysis. The PVA program acts as the system model (solid outline) to simulate individual survival and reproduction based on individual and population state variables (shown in italics) passed from other models. Epidemiological model (dashed outlines) simulates individual transitions in disease status. The central information flow control program passes state variables between the system and modifier models at appropriate time steps. Rounded rectangles represent software components, and parallelograms identify model output variables from Vortex.

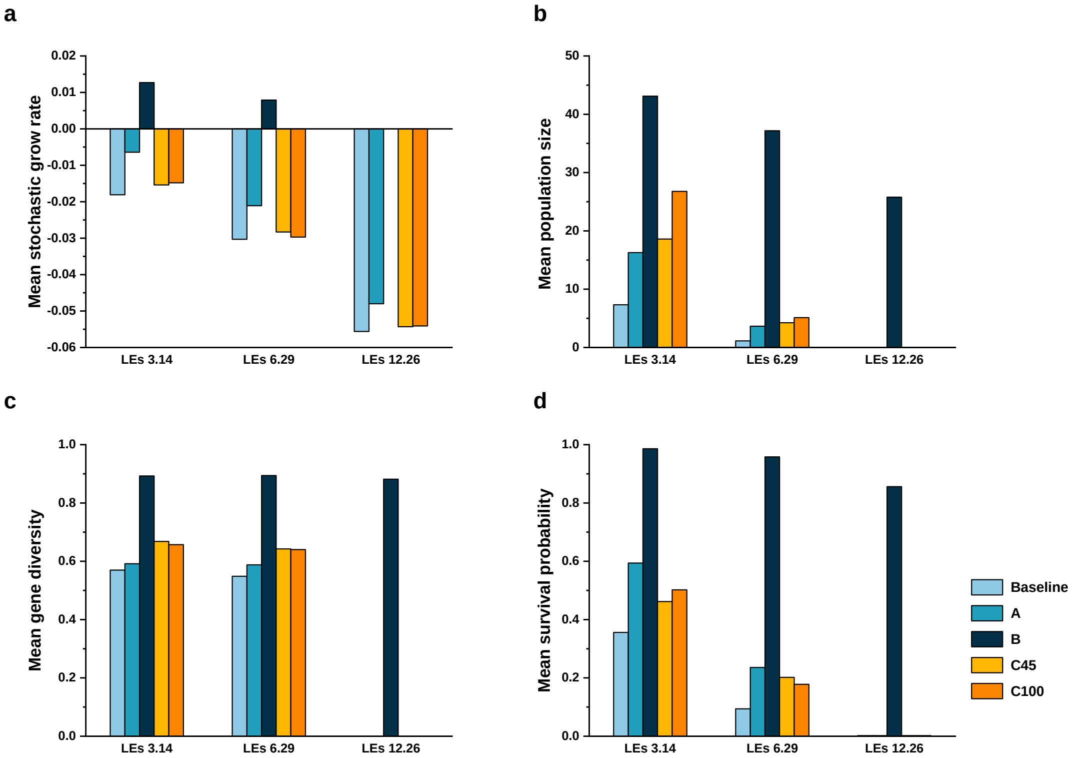

Figure 3. Estimates of stochastic population growth (a), population size (b), genetic diversity (c) and survival probability (d) for the small Amur tiger population under different management alternatives and lethal equivalents (LEs) over 100 years based on the average of 500 model runs. Scenario A: dog control in the Amur tiger habitat; Scenario B: establish habitat connectivity between large and small populations; Scenario C45: habitat expanded to accommodate 45 females; Scenario C100: habitat expanded to accommodate 100 females.

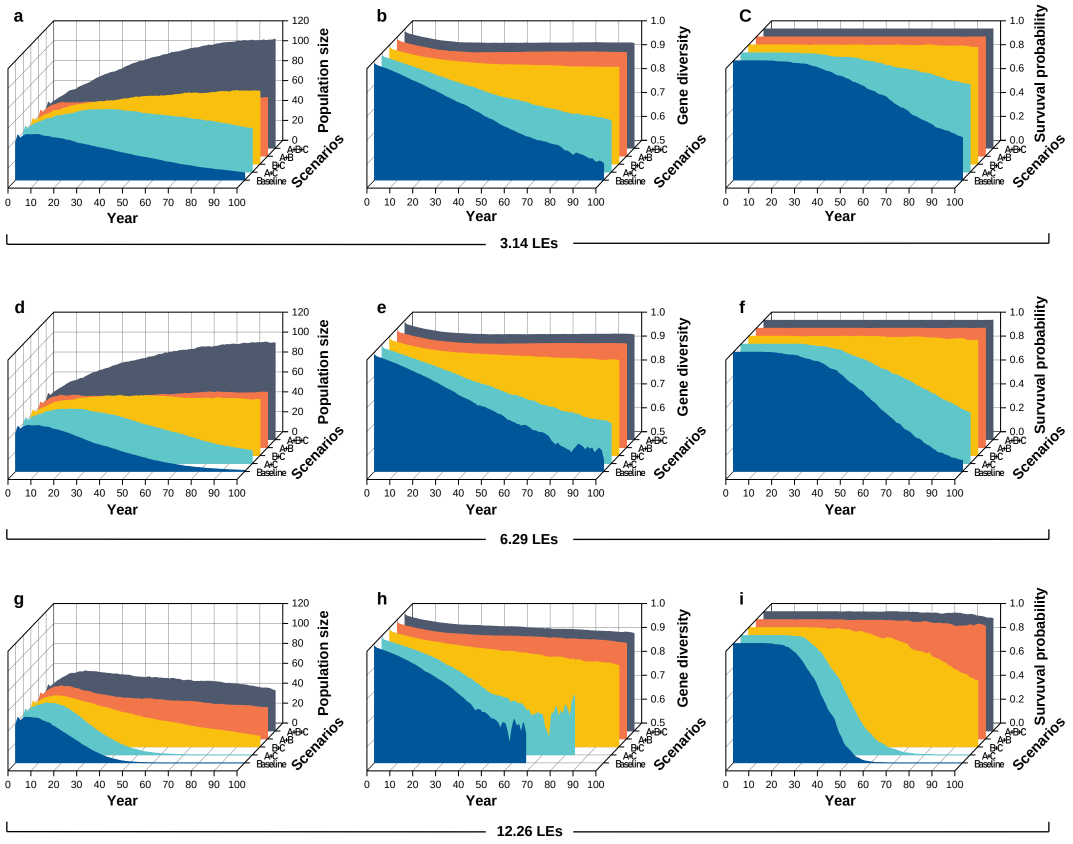

Figure 4. Changes in population size, genetic diversity, and survival probability of small Amur tiger population under different combinations of management actions and lethal equivalents (LEs) over 100 years based on the average of 500 model runs. Scenario A: dog control in the Amur tiger habitat; Scenario B: establish habitat connectivity between large and small populations; Scenario C: habitat expanded to accommodate 45 females.