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

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1 **Addressing the impact of canine distemper spreading on an isolated**

2 **tiger population in northeast Asia**

3 **Running title: PVA of Amur tiger population**

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Abstract

26

27   The continuation of the isolated Amur tiger (*Panthera tigris altaica*) population

28   living on the China-Russia border is facing serious challenges due to factors such as its

29   small size (including 38 individuals) and canine distemper virus (CDV). To assess

30   options to reduce the impact of these negative factors, we use a population viability

31   analysis (PVA) metamodel, which consists of a traditional individual-based

32   demographic model linked to an epidemiological model, to assess options for

33   controlling the impact of negative factors through domestic dog management in

34   protected areas, increasing connectivity to the neighboring large population (including

35   more than 400 individuals) and habitat expansion. Without intervention, under

36   inbreeding depression of 3.14, 6.29 and 12.26 lethal equivalents, our metamodel

37   predicted the extinction within 100 years is 64.4%, 90.6% and 99.8%, respectively. In

38   addition, the simulation results showed that dog management or habitat expansion

39   independently will not ensure tiger population viability for the next 100 years, and

40   connectivity to the neighboring population would only keep the population size from

41   rapidly declining. However, when the above three conservation scenarios are combined,

42   even at the highest level of 12.26 lethal equivalents inbreeding depression, population

43   size will not decline, the probability of extinction will be < 5.8%. Our findings highlight

44   that protecting the Amur tiger necessitates a multifaceted synergistic effort. Our key

45   management recommendations for this population underline the importance of reducing

46   CDV threats and expanding tiger occupancy to its former range in China, but

47   re-establishing habitat connectivity to the neighboring population is an important

48   long-term objective.

49

50   **Keywords**: Amur tiger; Canine distemper virus; Habitat connectivity; Metamodel;

51   Population viability analysis (PVA)

52   **1 INTRODUCTION**

53   The tiger (*Panthera tigris*), a flagship species in Asia, has declined to fewer than

54   5,000 individuals remaining in less than 7% of the surface of its historical range (Joshi

55   *et al.* 2016; Jhala *et al.* 2021). Among the five extant subspecies, the Amur or Siberian

56   tiger (*P. t. altaica*) is the northernmost (Wang *et al.* 2018). It suffered a severe decline in

57   the mid-20th century, and currently has a low level of genetic diversity (Henry *et al.*

58   2009; Dou *et al.* 2016). Fewer than 550 wild Amur tigers exist; they are distributed in

59   two populations separated by urban conglomerates and highways (Miquelle *et al.* 2007;

60   Wang *et al.* 2018). The larger population is spread widely in the Sikhote-Alin mountains,

61   Russia, and the smaller isolated Changbai-Primorye population (< 40 tigers) is restricted

62   to the China-Russia border (Hebblewhite *et al.* 2014; Feng *et al.* 2017). The

63   Changbai-Primorye population represents the main source for recovery of the Amur

64   tiger in much of its former range in northeast China (Miquelle *et al.* 2010; Wang *et al.*

65   2016; Qi *et al.* 2021).

66   Unfortunately, this population is currently facing multiple threats, including

67   insufficient prey resources (Wang *et al.* 2018), fragmentation and degradation of habitat

68   (Hebblewhite *et al.* 2014; Wang *et al.* 2016), poaching (Robinson *et al.* 2015), and

69   inbreeding depression (Henry *et al.* 2009; Ning *et al.* 2021). Furthermore, recent studies

70   have shown that tiger populations are facing an emerging threat from canine distemper

71   virus (CDV). CDV is a nearly globally distributed RNA virus (Deem *et al.* 2000;

72   Adhikari *et al.* 2020) that has caused significant decline in carnivore populations such

73   as Serengeti lions (*P. leo*) (Roelke-Parker *et al.* 1996; Weckworth *et al.* 2020) and

74   Ethiopian wolves (*Canis simensis*) (Gordon *et al.* 2015). As early as 2000, CDV was

75   reported in the Sikhote-Alin Amur tiger population (Quigley *et al.* 2010; Gilbert *et al.*

76   2015), and CDV was a factor responsible for a rapid decline of the Sikhote-Alin

77   population (Miquelle *et al.* 2015). Although not yet detected in the Changbai-Primorye

78   population, studies have shown that CDV has been spreading within sympatric

79   population of Amur leopard (*P. pardus orientalis*) (Sulikhan *et al.* 2018). The

80   consequences of CDV spread to Changbai-Primorye Amur tiger population could be

81   devastating. The multi-host nature of CDV poses a great threat to felid populations that

82   coexist with other hosts. For the Sikhote-Alin and Changbai-Primorye tiger populations,

83   free roaming domestic dogs that are occasionally killed by tigers (Sugimoto *et al.* 2016;

84   Dou *et al.* 2019) constitutes a potential reservoir of infection for tigers (Craft *et al.*

85   2009), who provide 3-6% of the biomass consumed of tigers (Gu *et al.* 2018; Dou *et al.*

86   2019). Few studies have assessed the impact of CDV on a critically small endangered

87   tiger population.

88   Currently, China and Russia are cooperating to conserve this population through

89   joint monitoring (Feng *et al.* 2017). Additionally, in 2016, the Chinese government

90   established a National Park, that expanded three Amur tiger and leopard reserves in

91   China to create a ~15,000 km^2 Northeast Tiger Leopard National Park. This expansion

92   is linked to the Land of Leopard Reserve, Russia, which has formed an 18,000 km^2

93   landscape for large felids. However, human development has effectively blocked

94   continuous genetic exchange between Changbai-Primorye and the Sikhote-Alin

95   population, increasing the risk of inbreeding depression in the Changbai-Primorye

96   population (Henry *et al.* 2009; Sorokin *et al.* 2016).

97   Given the isolation and low genetic diversity of this population and the specific

98   threats of CDV, a population viability analysis (PVA) is urgently needed for the

99   Changbai-Primorye tiger population. Previous PVAs of the Amur tiger assessed the

100   impact of habitat connectivity and fragmentation (Carroll & Miquelle 2006; Tian *et al.*

101   2011), and the influence of CDV on the larger Sikhote-Alin population (Gilbert *et al.*

102   2020). However, when CDV and other wildlife diseases are incorporated in PVA models

103   they are usually treated as a general random effect and operate at the same time scale as

104   the PVA. Epidemic disease such as CDV have dynamics that are often strongly related

105   to the specific host populations and they operate at a rapid temporal scale not captured

106   in a typical PVA analysis using an annual time step (Smith *et al.* 2009; Shoemaker *et al.*

107   2014). Therefore, in this study, we modeled the viability of the Changbai-Primorye tiger

108   population combining a traditional PVA (Lacy & Miller 2020) with a separate CDV

109   epidemiological model (Lacy *et al.* 2020). This metamodel approach is commonly used

110   to simulate the spread of epidemic diseases within wild populations (Bradshaw *et al.*

111   2012).

112   Here, we assess the probability of the persistence of the Changbai-Primorye

113   population for the next 100 years. We (i) use a metamodel modelling approach to

114   determine the impact of CDV infection, lack of connectivity and restricted habitat

115   which threaten the long-term viability of this population and (ii) assess the most

116   effective combinations of management strategies that increase CDV infection control,

117   expand habitat into its former range in China and establish population connectivity with

118   the larger Sikhote-Alin population. Our results provide guidance for conservation

119   policies to enhance the viability of the Changbai-Primorye population.

120   **2 MATERIALS AND METHODS**

121   **2.1 Study area**

122   The smaller Changbai-Primorye tiger population occurs in the Changbai Mountains

123   in the Jilin and Heilongjiang provinces of China and in the Land of Leopards National

124   Park in southwestern Primorye Province (Figure 1). The Changbai Mountains are one of

125   the highest priority Conservation Areas in China. This landscape consists of a large

126   network of habitat patches, which are connected with the Land of Leopards National

127   Park in Russia (Hebblewhite *et al.* 2012). In 2015, based on long-term monitoring, we

128   estimated the Changbai-Primorye population contained at least 38 tigers (13 adult

129   females, 10 adult males, 3 unidentified adults, and 12 sub-adults/cubs) occupying 9,000

130   km^2 along the China-Russia border (Feng *et al.* 2017). The elevations of the rugged

131   landscape ranges from 5m to 1477 m and has a temperate continental monsoon climate

132   that supports a temperate coniferous broad-leaved mixed forest. Due to long-term

133   deforestation, many low-elevation forests in these areas have been transformed into

134 secondary deciduous forests (Wang *et al.* 2016). The main prey species of Amur tigers

135 in this area are wild boar (*Sus scrofa*), sika deer (*Cervus nippon*), Siberian roe deer

136 (*Capreolus pygargus*), and domesticated species, such as cows and dogs (Kerley *et al.*

137 2015). The area has been subjected to cattle grazing, ginseng planting, frog farming, and

138 edible fern collection for decades, particularly on the Chinese side (Feng *et al.* 2021).

139 **2.2 Modelling overview**

140 We developed a metamodel using two spatially implicit submodels to assess the

141 extinction risk of the tiger population (Figure 2): an age- and sex-structured,

142 individual-based stochastic demographic model based on Vortex software (version

143 10.5.0) (Lacy & Miller 2020) and an individual-based epidemiological model that

144 simulates epizootics such as CDV built with Outbreak software (version 2.11.0) (Lacy

145 *et al.* 2020). The two submodels were connected by the Metamodel Manager (version

146 1.0.6) (Pollak & Lacy 2020), which transfers information back and forth between

147 submodels as "open data" that are updated by each before being passed on. All

148 scenarios were projected for 100 years, with 500 model runs, each one with a specific

149 draw of parameter values from its probability distributions or specified; the results of

150 population size and genetic diversity were averaged across the runs. The population

151 survival probability was calculated as the percentage of simulations ending with

152 population survival.

153 **2.2.1 Tiger demographic model**

154 We used Vortex to build a demographic model for the tiger population with one

155 year as a time step. Cubs and juveniles do not maintain their own territories (Tian *et al.*

156 2011) and male territories overlap with those of 1-3 females, while the overlap between

157 females is relatively low (Hernandez-Blanco *et al.* 2015; Xiao *et al.* 2016). Thus, in this

158 study, the habitat carrying capacity was measured in terms of female tiger home ranges;

159 the initial habitat of 9,000 km^2 can accommodate approximately 23 females with an

160 average home range of approximately 400 km^2 (Hernandez-Blanco *et al.* 2015). The

161   gestation period of the Amur tiger is 95-100 days, and the time of caring for the cubs is

162   approximately 18.8 months (Kerley *et al.* 2003). So, we used 2 years both for time that

163   young were dependent on their mother and the interbirth interval. If a female tiger died,

164   all of her currently dependent offspring also died. For the mortality rates of the Amur

165   tiger, we refer to mortality data from 1992 to 2012 in the Sikhote-Alin Mountains,

166   Russia (Robinson *et al.* 2015). Poaching has been a severe threat to wild tiger survival

167   (Kenney et al. 1995), but because of the Changbai-Primorye population's strong

168   protection and transboundary cooperation, we used a mortality rate of subadults and

169   adults as the sum of the natural mortality rate (5.1%) and 50% of the Sikhote-Alin

170   population's poaching death rate (10.3%) (Robinson *et al.* 2015). In addition, inbreeding

171   depression has been confirmed to exist in wild tiger populations (Smith & Mcdougal

172   1991), and the Amur tiger population in China has reached a moderate level of

173   inbreeding (Ning *et al.* 2021), but accurate lethal equivalents to measure the severity of

174   inbreeding depression have not been available. So we conservatively set the base line

175   lethal equivalents to 3.14 (Ralls *et al.* 1988) and then examine the impact of higher

176   lethal equivalents rated (6.29 and 12.26) more recently estimated by O'Grady et al.

177   (2006). Other model parameters are from previously reported tiger studies (see Table 1,

178   Appendix S1 for the details and main parameter input).

179   **2.2.2 Epidemiological modelling**

180   We developed an individual-based epidemiological model with one day as a time

181   step using Outbreak, to simulate CDV transmission in the tiger population in the

182   low-risk outbreak year. The model incorporates complex processes such as

183   interindividual transmission, pathogen environmental transmission, incubation period,

184   infection period and infection outcome. In the model, there are two main ways for tigers

185   to become infected with CDV: (i) contact with environmental disease sources, such as

186   predation on small and medium-sized wild predators and dogs carrying the virus or (ii)

187   intraspecific transmission through social contact. According to Gilbert et al. (2014), the

188   probability of CDV infection of Amur tigers by feeding on infected domestic dogs or

189   small carnivores is 1.4%, and the average daily infection probability is 0.003836%

190   (Appendix S2: Table S1). We set the probability of infection in the interaction process

191   as 1.4% of the cumulative prevalence rate of CDV within one year (see Table 2,

192   Appendix S2 for the details and main parameter input). Furthermore, to simulate CDV's

193   cyclical high-risk prevalence (Roscoe 1993), we applied 5 years of cyclically high

194   infection risk to the model (Gilbert *et al.* 2014). In the high risk outbreak year, we set an

195   additional mortality rate of 11.48% in the "catastrophes" module of Vortex (Table 1).

196   **2.3 Sensitivity analysis**

197   We developed a set of scenarios to assess how uncertainty about parameter values

198   affect metamodel outcomes. We tested 9 key parameters in the sensitivity analysis. For

199   lethal equivalents (LEs), in addition to a base line rate of 3.14, we examined values of

200   6.29 and 12.26 estimated through meta-analyses of multiple wild species (O'Grady et al.

201   2006; Kenney et al. 2014). To evaluate the impact of temporal high-risk cycles of CDV

202   infection (CCI) we used cycles of 3, 7 and no high infection cycle. For poaching

203   intensity (PI) we tested poaching mortality rates of 0 and 10.3% as reported by

204   Robinson et al. (2015) (see Appendix S1 for the details). For the other 6 parameters,

205   mortality rate after CDV infection (MCI), successfully breeding female proportion

206   (BFP), infant-cub (0-1 year old) mortality rate (IMR), adult (>3 years old) female

207   mortality rate (FMR), adult (>3 years old) male mortality rate (MMR), and carrying

208   capacity (K), we increased or decreased the baseline value by 40% (He *et al.* 2020). A

209   total of 19 scenarios were created for this analysis. We varied each key parameter while

210   holding all other parameters to baseline values. The outputs of each sensitive scenario

211   were compared to the baseline scenario: mean stochastic population growth rate (R),

212   mean population number at the 100th year (N), population genetic diversity at the 100th

213   year (GD), probability of extinction (PE), and mean time of extinction (TE). The

214   sensitivity index (Pulliam *et al.* 1992) of the mean stochastic population growth rate for

215   each simulation parameter was calculated as follows:

216 $$S_R = | (\Delta R / R) / (\Delta P / P) |$$

217     $\Delta R/R$ represents the variable ratio of the mean stochastic population growth rate over

218   100 years; $\Delta P/P$ represents the variable ratio of the parameters. The sensitivity index is

219   proportional to the influence of the parameters on the output of the model.

220   **2.4 Tests of alternative management actions**

221   Based on the recent threats faced by the Amur tiger, we developed three scenarios

222   to assess how different management actions and their combinations affect the

223   probability of extinction of the Changbai-Primorye population (Appendix S4: Table S1

224   and Appendix S3).

225   *Scenario A: CDV control*

226   For Scenario A, we reduced the risk of CDV infection in Amur tigers by managing

227   free-ranging domestic dogs (e.g., vaccination, hereafter referred to as "dog control").

228   The probability of the tiger being infected with CDV due to predation on dogs was

229   reduced to 0, the probability of CDV transmission between individuals in low-risk years

230   was 0.99%, the daily average pathogenic environmental infection probability was

231   0.002712%, and the mortality rate of CDV infection in high-risk years was 83.8%.

232   These parameters were derived from published studies on the influence of CDV on

233   Amur tigers (Gilbert *et al.* 2014, 2015).

234   *Scenario B: habitat connectivity*

235   For Scenario B, we constructed a larger population (the initial population contains

236   454 individuals and the habitat can hold 502 adult female tigers) in the model, based on

237   the population characteristics of the neighboring larger Sikhote-Alin population. Then

238   we established habitat connectivity between large and small populations by exchanging

239   individuals between populations. According to the research of Henry et al. (2009),

240   before the complete separation of the two populations, the probability of individuals in

241   the large population dispersing to the small population is 0.22%, and the probability of

242 individuals in the small population dispersing to the large population is 1.3%. In the

243 model we use this pair of dispersion rates.

244 *Scenario C: habitat expansion*

245 Scenario C was divided into two options. For the first option scenario C45, tiger

246 habitat increased to 18,000 km^2 within 20 years, which could accommodate 45 female

247 tigers, based on the plan of Wang *et al.* (2018) that designated protected habitat

248 becomes occupied. For the second option scenario C100, tiger habitat increased to

249 40,000 km^2 in 30 years and can accommodate 100 female tigers, based on Hebblewhite

250 et al.'s (2012) estimate of potential recoverable core habitat in China (see Appendix S3).

251 **2.5 Inbreeding depression**

252 To avoid underestimating the degree of inbreeding depression in wildlife

253 populations, in addition to the inbreeding depression test for 3.14LEs, we also examined

254 the impact of 6.29 LEs based on Kenney et al. (2014) and 12.26 LEs based on O'Grady

255 et al. (2006), to assess population trends under different cases of inbreeding depression.

256 We set the absence of any management alternatives as the baseline for each inbreeding

257 depression scenario. In the simulation of 3.14 LEs, the inbreeding only affected the

258 first-year survival. In the simulation of 6.29 LEs, 3.94 LEs were used to impact

259 fecundity and 2.35 LEs to reduce first-year survival. In the simulation of 12.26 LEs, we

260 added 5.97 LEs for altering survival from age 1 to sexual maturity based on 6.29 LEs.

261 **3 RESULTS**

262 **3.1 Baseline scenario**

263 The baseline scenario (no management actions) predicted that under inbreeding

264 depression of 3.14 LEs, the small population would decrease at a mean rate of 0.018 per

265 year, and would have a 64.4% extinction probability within 100 years. The mean time of

266 extinction was 66 years, the mean population size was 7 individuals and the population

267 genetic diversity would decline to 57.0% of its original level (Table 3).

268 **3.2 Sensitivity analysis**

269   The results showed that the three parameters with the highest sensitivity indices

270   were BFP, MCI and IMR (Table 3, Figure S1 in Appendix S4). The effect of different

271   parameter variations on the simulation were as follows: for LEs of 6.29 and 12.26, the

272   extinction probability at 100 years was 90.6% and 99.8%, respectively and mean

273   population size declined to 1 and 0, respectively (Table 3). For CCI, the longer the

274   interval between high infection rates, the slower the population declines. However,

275   when the infectious cycle increased to 7 years, the population extinction probability was

276   still high (43%), but when cycle of CDV high infection risk was removed, the

277   probability of extinction dropped to 0, and the population slowly grew from an initial

278   size of 38 to 58 individuals after 100 years. For PI, when the mortality caused by

279   poaching was set at 0% and 10.3%, the extinction probability was 1.8% and 99.8%,

280   respectively. When poaching was fully eradicated, the population grew slowly, reaching

281   a size of 56 after 100 years. The population exhibited a growing trend when MCI, IMR,

282   and FMR were reduced by 40% and BFP was increased by 40%. For MMR and K, their

283   increase or decrease had little influence on the population (Table 3).

284   **3.2 Tests of alternative management actions**

285   Just reducing domestic dogs (scenario A), even in the mildest inbreeding depression

286   category (3.14 LEs), resulted in a negative growth rate (-0.006), the population

287   extinction probability was 40.6%, and the population size declined to 16 within the 100

288   years. In the other two more severe inbreeding depression cases, the population is at a

289   high risk of extinction, with extinction probability above 75% (Figure 3 and Table S2 in

290   Appendix S4).

291   Increasing habitat connectivity (scenario B), with inbreeding depression at 3.14 and

292   6.29 LEs, resulted in a mean stochastic growth rate was 0.013 and 0.008, the mean

293   population genetic diversity all declined to 89%, the population size reached 43 and 37,

294   and the extinction probability within 100 years dropped to 1.4% and 4.2%, respectively.

295   However, in the case of 12.26 LEs, the mean stochastic growth rate was 0 and the

296   extinction probability was 14.4% (Figure 3 and Table S2 in Appendix S4).

297   Expanding the tiger's range (scenario C) alone was inadequate. For both schemes

298   (C45, C100), the simulation results were essentially the same as the baseline under the

299   different inbreeding depression, except for a slight difference in population size in the

300   100th year. The population remained at high risk of extinction (Figure 3 and Table S2 in

301   Appendix S4).

302   In summary, as the value of LEs increases, the benefits of implementing just one of

303   the scenarios was largely ineffective. Habitat connectivity provided the biggest benefit.

304   Implementing both habitat expansion and reducing the number of dogs in the forest

305   have smaller benefits, but increasing habitat is the least beneficial (Figure 3). We chose

306   the expansion scheme of 45 females (C45) as the representative of the habitat expansion

307   scenario and simulated four combinations of the three scenarios overlapping each other.

308   We found that the benefits of the four combinations were much higher than those of

309   single management action (Appendix S4: Table S2, Table S3), regardless of the LEs

310   (Figure 4). In the combination of scenario A and C at three levels of LEs, the population

311   size reached 44, 13 and 0 within the 100th year, the genetic diversity was 71.3%, 66.7%,

312   0.00%, the mean stochastic growth rate was -0.002, -0.018, and -0.049, and the

313   population extinction probability was 26.4%, 57.8%, and 99.8%, respectively; in the

314   combination of scenarios B and C with the 3 possible levels of LEs, the population size

315   was 73, 56, and 11, and the genetic diversity was 90.5%, 89.7%, and 88.4%,

316   respectively, the mean stochastic growth rate was 0.008, 0.003, and -0.016, and the

317   extinction probability was 2.2%, 3.4%, and 44.2% within 100 years, respectively; in the

318   combination of scenario A and B of three levels LE, the population size was 59, 56, 32,

319   the genetic diversity in the 100th year was 93.3%, 93.3%, and 90.0%, and the mean

320   stochastic growth rate was 0.030, 0.024, and 0.004, respectively. And there was no risk

321   of population extinction within 100 years in the 3.14 and 6.29 LEs but the extinction

322   probability with 12.26 LEs was 5.6%; when the three actions were combined, the

323 population size was 110, 97, 41, genetic diversity in the 100th year was 93.8%, 93.8%,

324 91.1%, and the mean stochastic growth rate was 0.021, 0.016, and 0.005, respectively.

325 There was no risk of extinction in the 3.14 and 6.29 LEs cases, but the extinction

326 probability with 12.26 LEs was 5.6% (Appendix S4: Table S3).

327 **4 DISCUSSIONS**

328   By incorporating a metamodel, we were better able to capture the potential

329 dynamics of the rapid spread of CDV within the Changbai-Primorye tiger population

330 and thus obtain a more realistic prediction of the impact of CDV on tigers. Compared

331 with previous PVA tiger studies (Carroll & Miquelle 2006; Tian *et al.* 2011), the

332 contributions of our study are as follows: (i) the metamodel allowed us to incorporate

333 the detailed, rapid dynamics of CDV into a tiger PVA, (ii) we incorporated recent

334 estimates of inbreeding depression that may be more realistic than those used in

335 previous models, and (iii) under these different levels of inbreeding depression and a

336 realistic model of CDV, we were able to explore management options for recovery of

337 the Changbai-Primorye tiger population. Through the simulation of different

338 management measures and their combinations, our results clearly show the importance

339 of habitat connectivity.

340 **4.1 Insights from sensitivity assessment**

341   Our results highlighted that with an outbreak of CDV, this population may require a

342 combination of management strategies to insure its persistence. The extinction

343 probability was greater than 60% under all realistic baseline estimations of lethal

344 equivalents without any intervention. Sensitivity analysis examined the impact of

345 variation in key demographic parameters on the model output results. Variation in the

346 proportion of breeding females was the most sensitive parameter in our sensitivity

347 analysis but based on observations in Nepal and Thailand (James L.D. Smith pers.

348 comm.) there is actually little variation in proportion of females that get pregnant. In

349 contrast, variation in female and infant-juvenile mortality does occur in wild

350   populations and can have a strong negative impact of recruitment. In tigers and other

351   large felids, female survival is a major determinant of population viability (Kenney et al.

352   2014). This finding is consistent with PVA studies of other mammals such as the fennec

353   fox (*Vulpes zerda*), the Asian elephant (*Elephas maximus*) (He *et al.* 2020; Franklin *et al.*

354   2021). Therefore, it is critical to ensure female tigers have good breeding habitat and

355   low human-caused mortality to help increase their survival rates (Miquelle *et al.* 2015).

356   Sensitivity analysis also highlighted that poaching intensity, cycles of CDV high

357   infection risk and mortality rate after CDV infection all had critical impacts on the

358   probability of extinction. Without the threat of poaching and CDV, the current

359   population would most likely remain viable for the next 100 years.

360   The sensitivity analysis showed that changes in environmental carrying capacity did

361   not reduce the probability of extinction. This could be because the Changbai-Primorye

362   population has been kept below the environmental capacity for long periods of time due

363   to multiple threats (Robinson *et al.* 2015; Wang *et al.* 2018; Ning *et al.* 2021), and the

364   influence of inbreeding depression did not decline with habitat expansion. Even if with

365   a large enough habitat, it is difficult for the population to spread to any additional

366   habitat due to the high extinction risk within the population.

367   Given the difficulty in estimating rates of inbreeding depression in the wild and

368   recent debate as to the extent to which purging reduces inbreeding depression

369   (Armstrong *et al.* 2021), further research is needed to estimate current levels of

370   inbreeding depression in tigers and other species. Alternatively, we may have

371   over-estimated mortality of adult females in our model and that is restricting recovery.

372   Kenney et al. (2014) estimated a much higher annual rate of adult female survival than

373   we used in our model. Future modeling of this population will benefit from efforts to

374   improve estimation of this parameter through our current intensive camera trapping.

375   Simultaneously, it is critical to monitor CDV in both tigers and domestic species.

376   **4.2 Management interventions**

377   With the newly established the Northeast Tiger and Leopard National Park in China,

378   tigers are now expanding their range into northeast China. However, the distribution

379   further from the Russian border is still spotty and the number of tigers is low (Wang *et*

380   *al.* 2016; Qi *et al.* 2021). Most of the habitat expansion in China is by young males.

381   Female tigers and their young are confined to the China-Russia border and breeding

382   habitat is still estimated at < 6,000 km^2 (Wang *et al.* 2018; Qi *et al.* 2021). At this

383   juncture, urgent actions are needed.

384   Our study revealed that maintaining connectivity among the two populations was

385   essential and a prerequisite for preventing drastic reduction of population. The

386   simulation of different management scenarios showed that habitat connectivity was the

387   only measure that effectively increased growth rates in the tiger population. Moreover,

388   the scenarios combining habitat connectivity performed relatively well in population

389   projections. In contrast, dog control, habitat expansion and this combination resulted in

390   the population reaching its maximum size in less than 40 years and then gradually

391   declining. It is thus clear that gene exchange among populations plays a key role in the

392   recovery and long-term population persistence.

393   A true barrier now exists due to continuing development along the Razdolnaya

394   River basin, which prevents movements of tigers between the Changbai landscape and

395   the southern Sikhote-Alin landscape; the populations show clear genetic differentiation

396   (Sorokin *et al.* 2016). Furthermore, a recent study reported poor health status for the

397   Changbai-Primorye population as well as 50% of individual relationships were cousins

398   or half-sibs (Ning *et al.* 2021). Miquelle et al. (2015) used least-cost distance analyses

399   to identify a single potential corridor to retain connectivity for the two subpopulations,

400   but no evidence demonstrates that this corridor is actually used by tigers. When habitat

401   connectivity is difficult to achieve, a more immediate, and practical strategy, is

402   translocation of individuals from the Sikhote-Alin population. A similar movement of

403   Texas panthers into the Florida panther population (*P. c. coryi*) resulted in a dramatic

404 population recovery (Johnson *et al.* 2010; Hostetler *et al.* 2013). Similarly, the

405 reintroduction of tigers in Panna, India, resulted in rapid population recovery (Sankar *et*

406 *al.* 2010).

407 CDV infection is regarded as the main threat to large felids conservation not only in

408 Asia but also worldwide (Adhikari *et al.* 2020). Domestic dogs are a proven source of

409 CDV for wild animals and transmit the CDV to the tiger population through direct

410 predation by tigers or indirectly through interaction with other wildlife, which can

411 increase the mortality risk of tigers (Gilbert *et al.* 2014; Dou *et al.* 2019). However,

412 currently, domestic dogs have widely invaded into the Amur tiger's habitat (Gilbert *et al.*

413 2020). According to our camera-trapping data and field surveys, domestic dogs are still

414 entering the parkland and commited wildlife attacks in 2021; on the Chinese side,

415 unvaccinated domestic dogs had a high level of positive antibodies for CDV due to

416 exposure to the disease (37% in 202 domestic dogs serum tests in 2018, unpublished

417 data). Although dog management practices were not the most effective when compared

418 to habitat connectivity, and domestic dogs may not be the only source of CDV infection

419 (Gilbert *et al.* 2020), dog management was the easiest and safest method to achieve

420 among all conservation actions, and when combined with other measures, it can

421 effectively improve population trajectories by increasing the population recovery speed.

422 Given CDV is preventable, strict vaccination of domestic dogs with the commercial

423 attenuated vaccine is needed. To ensure the long-term success of tiger conservation, we

424 suggest that the local government implement policies aimed at gradually controlling

425 dogs, if not completely prohibiting all dogs in the tiger's core range.

426 Although the establishment of national park has expanded the habitat of Amur

427 tigers, through the monitoring of camera trap data in the past few years, the core range

428 of Amur tigers still stays at the Sino-Russian border and does not spread to China on a

429 large scale. As the results in our simulations show, the expansion of habitat did not

430 significantly increase the population size, especially in the case of severe inbreeding

431   depression. This may be due to the fact that the Amur tiger population face many threats,

432   such as low initial population size, inbreeding depression and CDV, which cause the

433   population size to remain below the carrying capacity for a long time. Even with

434   sufficiently large habitats, it is difficult for tiger population to spread due to the high

435   risk of extinction. The same result was obtained when assessing the extinction risk of

436   tigers in central India (Thatte *et al.* 2018). Although our model did not indicate that

437   habitat expansion alone would reduce the probability of extinction, habitat expansion

438   has several benefits that should not be overlooked. Habitat expansion would increase

439   structurally and spatial diversity of the landscape, which in turn might decrease the

440   spread of CDV. Also shifting from people intensive logging activities to conservation

441   management may reduce the impact of humans and their dogs serving as a vector for

442   CDV. In India, a topographically and vegetatively diverse landscape also reduced the

443   risk of extinction (Thatte *et al.* 2018).

444   In summary, our findings highlight the critical need for integrated conservation

445   strategies and actions that link wildlife populations, landscape planning, CDV research,

446   and international cooperation while also meeting human development goals. Our

447   modeling of the potential impact of CDV highlights the critical need for integrated

448   conservation strategies that link and expand wildlife populations, institute broad

449   landscape planning, and include continuous surveys of potential CDV outbreaks.

450   Fortunately, transborder cooperation in monitoring and management is already in place.

451   **4.3 Methodological considerations**

452   Metamodelling requires estimating a number of parameters to build each

453   submodel with an acceptable degree of realism, and hence there is a degree of

454   uncertainty associated with their results (Shoemaker *et al.* 2014). However, metamodels

455   can assist managers and policymakers in making decisions for the conservation of

456   endangered populations in an uncertain environment (Reed *et al.* 2002; Lawson *et al.*

457   2021). Therefore, this analysis provides the relative benefits of various possible actions

458 rather than an absolute and accurate prediction of future population trends. Inbreeding

459 could have an impact on the survival and reproduction of adult tigers, especially in the

460 face of changing environmental conditions (Coltman *et al.* 1999; Fox & Reed 2011),

461 and population connectivity may slightly mitigate inbreeding depression in populations.

462 However, the above two considerations were not included in the model because of the

463 difficulty of accurately estimating the relevant parameters and their limited influence on

464 the overall population trends. In addition, since prey resources are also an important

465 factor affecting tiger population continuation and management and policy decisions

466 operate on short-term projections, it is necessary to construct more complex and

467 shorter-term projections that include prey species in the future.

468

469 **REFERENCES**

470 Adhikari RB, Shrestha M, Puri G, Regmi GR & Ghimire TR (2020). Canine Distemper

471   Virus (CDV): an emerging threat to Nepal's wildlife. *Applied Science and*

472   *Technology Annals* **1**, 149–54.

473 Armstrong EE, Khan A, Taylor RW *et al.* (2021). Recent Evolutionary History of

474   Tigers Highlights Contrasting Roles of Genetic Drift and Selection. *Molecular*

475   *Biology and Evolution* **38**, 2366–79.

476 Bradshaw CJA, McMahon CR, Miller PS *et al.* (2012). Novel coupling of

477   individual-based epidemiological and demographic models predicts realistic

478   dynamics of tuberculosis in alien buffalo. *Journal of Applied Ecology* **49**,

479   268–77.

480 Carroll C & Miquelle DG (2006). Spatial viability analysis of Amur tiger Panthera tigris

481   altaica in the Russian Far East: the role of protected areas and landscape matrix

482   in population persistence. *Journal of Applied Ecology* **43**, 1056–68.

483   Coltman DW, Pilkington JG, Smith JA & Pemberton JM (1999). Parasite-mediated
484   selection against inbred Soay sheep in a free-living, island population. *Evolution*
485   **53**, 1259–67.

486   Craft ME, Volz E, Packer C & Meyers LA (2009). Distinguishing epidemic waves from
487   disease spillover in a wildlife population. *Proceedings of the Royal Society B:*
488   *Biological Sciences* **276**, 1777–85.

489   Deem SL, Spelman LH, Yates RA & Montali RJ (2000). Canine distemper in terrestrial
490   carnivores: A review. *Journal of Zoo and Wildlife Medicine* **31**, 441–51.

491   Dou H, Yang H, Feng L, Mou P, Wang T & Ge J (2016). Estimating the population size
492   and genetic diversity of Amur tigers in Northeast China. *PLOS ONE* **11**,
493   e0154254.

494   Dou H, Yang H, Smith JLD, Feng L, Wang T & Ge J (2019). Prey selection of Amur
495   tigers in relation to the spatiotemporal overlap with prey across the
496   Sino–Russian border. *Wildlife Biology* **2019**, 1–11.

497   Feng L, Shevtsova E, Vitkalova A *et al.* (2017). Collaboration brings hope for the last
498   Amur leopards. *Cat News* **65**, 20.

499   Feng R, Lü X, Xiao W *et al.* (2021). Effects of free-ranging livestock on sympatric
500   herbivores at fine spatiotemporal scales. *Landscape Ecology* **36**, 1441–1457.

501   Fox CW & Reed DH (2011). Inbreeding depression increases with environmental stress:
502   an experimental study and meta-analysis. *Evolution* **65**, 246–58.

503   Franklin AD, Lacy RC, Bauman KL, Traylor-Holzer K & Powell DM (2021).
504   Incorporating drivers of reproductive success improves population viability
505   analysis. *Animal Conservation* **24**, 386–400.

506   Gilbert M, Miquelle DG, Goodrich JM *et al.* (2014). Estimating the potential impact of
507   canine distemper virus on the Amur tiger population (*Panthera tigris altaica*) in
508   Russia. *PLOS ONE* **9**, e110811.

509   Gilbert M, Soutyrina SV, Seryodkin IV *et al.* (2015). Canine distemper virus as a threat
510   to wild tigers in Russia and across their range. *Integrative Zoology* **10**, 329–43.

511   Gilbert M, Sulikhan N, Uphyrkina O *et al.* (2020). Distemper, extinction, and
512   vaccination of the Amur tiger. *Proceedings of the National Academy of Sciences*
513   **117**, 31954–62.

514   Gordon CH, Banyard A, Hussein A *et al.* (2015). Canine distemper in endangered
515   Ethiopian wolves. *Emerging Infectious Diseases* 824–32.

516   Gu J, Yu L, Hua Y *et al.* (2018). A comparison of food habits and prey preferences of
517   Amur tiger (*Panthera tigris altaica*) at the southwest Primorskii Krai in Russia
518   and Hunchun in China. *Integrative Zoology* **13**, 595–603.

519   He C, Du J, Zhu D & Zhang L (2020). Population viability analysis of small population:
520   a case study for Asian elephant in China. *Integrative Zoology* **15**, 350–62.

521   Hebblewhite M, Miquelle DG, Robinson H *et al.* (2014). Including biotic interactions
522   with ungulate prey and humans improves habitat conservation modeling for
523   endangered Amur tigers in the Russian Far East. *Biological Conservation* **178**,
524   50–64.

525   Hebblewhite M, Zimmermann F, Li Z *et al.* (2012). Is there a future for Amur tigers in a
526   restored tiger conservation landscape in Northeast China? *Animal Conservation*
527   **15**, 579–92.

528   Henry P, Miquelle D, Sugimoto T, McCULLOUGH DR, Caccone A & Russello MA

529   (2009). In situ population structure and ex situ representation of the endangered

530   Amur tiger. *Molecular Ecology* **18**, 3173–84.

531   Hernandez-Blanco JA, Naidenko SV, Chistopolova MD *et al.* (2015). Social structure

532   and space use of Amur tigers (*Panthera tigris altaica*) in Southern Russian Far

533   East based on GPS telemetry data. *Integrative Zoology* **10**, 365–75.

534   Hostetler JA, Onorato DP, Jansen D & Oli MK (2013). A cat's tale: the impact of

535   genetic restoration on Florida panther population dynamics and persistence.

536   *Journal of Animal Ecology* **82**, 608–20.

537   Jhala Y, Gopal R, Mathur V *et al.* (2021). Recovery of tigers in India: Critical

538   introspection and potential lessons. *People and Nature* **3**, 281–93.

539   Johnson WE, Onorato DP, Roelke ME *et al.* (2010). Genetic restoration of the Florida

540   panther. *Science* **329**, 1641–5.

541   Joshi AR, Dinerstein E, Wikramanayake E *et al.* (2016). Tracking changes and

542   preventing loss in critical tiger habitat. *Science Advances* **2**, e1501675.

543   Kenney JS, Allendorf FW, McDougal C & Smith JLD (2014). How much gene flow is

544   needed to avoid inbreeding depression in wild tiger populations? *Proceedings of

545   the Royal Society B: Biological Sciences* **281**, 20133337.

546   Kenney JS, Smith JL, Starfield AM & McDougal CW (1995). The long-term effects of

547   tiger poaching on population viability. *Conservation Biology* **9**, 1127–33.

548   Kerley LL, Goodrich JM, Miquelle DG, Smirnov EN, Quigley HB & Hornocker MG

549   (2003). Reproductive Parameters of Wild Female Amur (Siberian) Tigers

550   (*Panthera tigris altaica*). *Journal of Mammalogy* **84**, 288–98.

551   Lacy RC & Miller PS (2020). Vortex: A stochastic simulation of the extinction process.

552   Version 10.5. Available from URL: https://scti.tools/downloads/.

553 Lacy RC, Pollak JP, Miller PS, Hungerford L & Bright P (2020). Outbreak. Version
554   2.10. Available from URL: https://scti.tools/downloads/.

555 Lawson AJ, Folt B, Tucker AM, Erickson F & McGowan CP (2021). Decision context
556   as a necessary component of population viability analysis assessments: response
557   to Chaudhary and Oli 2020. *Conservation Biology* **35**, 1683–85.

558 Miquelle DG, M. Goodrich J, L. Kerley L *et al.* (2010). Chapter 32 - Science-Based
559   Conservation of Amur Tigers in the Russian Far East and Northeast China. In:
560   *Tigers of the World (Second Edition)*, Noyes Series in Animal Behavior,
561   Ecology, Conservation, and Management (eds R Tilson & PJ Nyhus) pp. 403–23.
562   William Andrew Publishing, Boston.

563 Miquelle DG, Pikunov D, Y.M. D *et al.* (2007). 2005 Amur Tiger Census. *Cat News* **46**,
564   14–15.

565 Miquelle DG, Smirnov EN, Zaumyslova OYu, Soutyrina SV & Johnson DH (2015).
566   Population dynamics of Amur tigers (*Panthera tigris altaica*) in Sikhote-Alin
567   Biosphere Zapovednik: 1966–2012. *Integrative Zoology* **10**, 315–28.

568 Ning Y, Roberts NJ, Qi J *et al.* (2021). Inbreeding status and implications for Amur
569   tigers. *Animal Conservation*.

570 O'Grady JJ, Brook BW, Reed DH, Ballou JD, Tonkyn DW & Frankham R (2006).
571   Realistic levels of inbreeding depression strongly affect extinction risk in wild
572   populations. *Biological Conservation* **133**, 42–51.

573 Pollak JP & Lacy RC (2020). Metamodel manager. Version 1.0.6. Available from URL:
574   https://scti.tools/downloads/.

575   Pulliam HR, Dunning Jr. JB & Liu J (1992). Population Dynamics in Complex

576   Landscapes: A Case Study. *Ecological Applications* **2**, 165–77.

577   Qi J, Gu J, Ning Y *et al.* (2021). Integrated assessments call for establishing a

578   sustainable meta-population of Amur tigers in northeast Asia. *Biological*

579   *Conservation* **261**, 109250.

580   Quigley KS, Evermann JF, Leathers CW *et al.* (2010). Morbillivirus Infection in a Wild

581   Siberian Tiger in the Russian Far East. *Journal of Wildlife Diseases* **46**, 1252–6.

582   Ralls K, Ballou JD & Templeton A (1988). Estimates of Lethal Equivalents and the

583   Cost of Inbreeding in Mammals. *Conservation Biology* **2**, 185–93.

584   Reed JM, Mills LS, Dunning JB *et al.* (2002). Emerging Issues in Population Viability

585   Analysis. *Conservation Biology* **16**, 7–19.

586   Robinson HS, Goodrich JM, Miquelle DG, Miller CS & Seryodkin IV (2015). Mortality

587   of Amur tigers: The more things change, the more they stay the same.

588   *Integrative Zoology* **10**, 344–53.

589   Roelke-Parker ME, Munson L, Packer C *et al.* (1996). A canine distemper virus

590   epidemic in Serengeti lions (*Panthera leo*). *Nature* **379**, 441–5.

591   Roscoe DE (1993). Epizootiology of canine distemper in new jersey raccoons. *Journal*

592   *of Wildlife Diseases* **29**, 390–5.

593   Sankar K, Qureshi Q, Nigam P *et al.* (2010). Monitoring of reintroduced tigers in

594   Sariska Tiger Reserve, Western India: preliminary findings on home range, prey

595   selection and food habits. *Tropical Conservation Science* **3**, 301–18.

596   Shoemaker KT, Lacy RC, Verant ML *et al.* (2014). Effects of prey metapopulation

597   structure on the viability of black-footed ferrets in plague-impacted landscapes:

598   a metamodelling approach. *Journal of Applied Ecology* **51**, 735–45.

599   Smith JLD & Mcdougal C (1991). The contribution of variance in lifetime reproduction

600   to effective population-size in tigers. *Conservation Biology* **5**, 484–90.

601   Smith KF, Acevedo-Whitehouse K & Pedersen AB (2009). The role of infectious

602   diseases in biological conservation. *Animal Conservation* **12**, 1–12.

603   Sorokin PA, Rozhnov VV, Krasnenko AU, Lukarevskiy VS, Naidenko SV &

604   Hernandez-Blanco JA (2016). Genetic structure of the Amur tiger (*Panthera*

605   *tigris altaica*) population: Are tigers in Sikhote-Alin and southwest Primorye

606   truly isolated? *Integrative Zoology* **11**, 25–32.

607   Sugimoto T, Aramilev VV, Nagata J & McCullough DR (2016). Winter food habits of

608   sympatric carnivores, Amur tigers and Far Eastern leopards, in the Russian Far

609   East. *Mammalian Biology* **81**, 214–8.

610   Sulikhan NS, Gilbert M, Blidchenko EY *et al.* (2018). Canine distemper virus in a wild

611   Far Eastern leopard (*Panthera pardus orientalis*). *Journal of Wildlife Diseases*

612   **54**, 170–4.

613   Thatte P, Joshi A, Vaidyanathan S, Landguth E & Ramakrishnan U (2018). Maintaining

614   tiger connectivity and minimizing extinction into the next century: Insights from

615   landscape genetics and spatially-explicit simulations. *Biological Conservation*

616   **218**, 181–91.

617   Tian Y, Wu J, Smith AT, Wang T, Kou X & Ge J (2011). Population viability of the

618   Siberian Tiger in a changing landscape: Going, going and gone? *Ecological*

619   *Modelling* **222**, 3166–80.

620   Wang T, Andrew Royle J, Smith JLD *et al.* (2018). Living on the edge: Opportunities

621   for Amur tiger recovery in China. *Biological Conservation* **217**, 269–79.

622 Wang T, Feng L, Mou P *et al.* (2016). Amur tigers and leopards returning to China:

623   direct evidence and a landscape conservation plan. *Landscape Ecology* **31**,

624   491–503.

625 Weckworth JK, Davis BW, Dubovi E *et al.* (2020). Cross-species transmission and

626   evolutionary dynamics of canine distemper virus during a spillover in African

627   lions of Serengeti National Park. *Molecular Ecology* **29**, 4308–21.

628 Xiao W, Feng L, Mou P *et al.* (2016). Estimating abundance and density of Amur tigers

629   along the Sino–Russian border. *Integrative Zoology* **11**, 322–32.

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

631 **Table 2.** Parameters input for the baseline scenario of the canine distemper epidemiological

632 model in Outbreak.

633

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

634 **Table 3.** Baseline candidate model results. R(SD): mean (standard deviation) of stochastic

635 population growth rate across all years and iterations; N (SD): mean (standard deviation) of

636 number of tigers at year 100th; GD (SD): initial genetic diversity (heterozygosity) remaining

637 in population at year 100th; PE: probability of extinction, defined as only 1 sex remains at

638 year 100th; TE: mean time of extinction (in years) for all iterations that went extinct within

639 100 years; SR: The sensitivity index of the mean stochastic population growth rate for each

640 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	

641
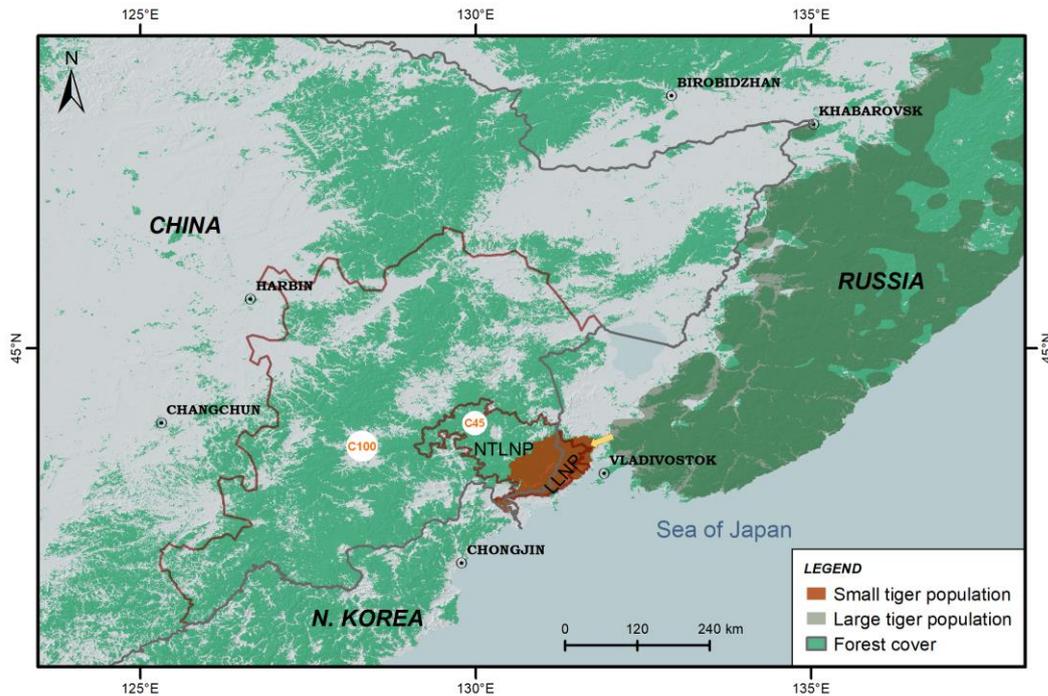
642   **Figure 1.** Current range of the Amur tiger in Northeast China and Far East Russia. Small

643   tiger population is areas with confirmed tiger breeding activity within the last 10 years. C100

644   and C45 indicate two habitat expansion schemes (see method for details). NTLNP and LLNP

645   is the Northeast Tiger and Leopard National Park of China and the Land of Leopard National

646   Park of Russia, respectively. Yellow arrow represents potential important ecological corridors

647   for tigers between small and large populations.

648
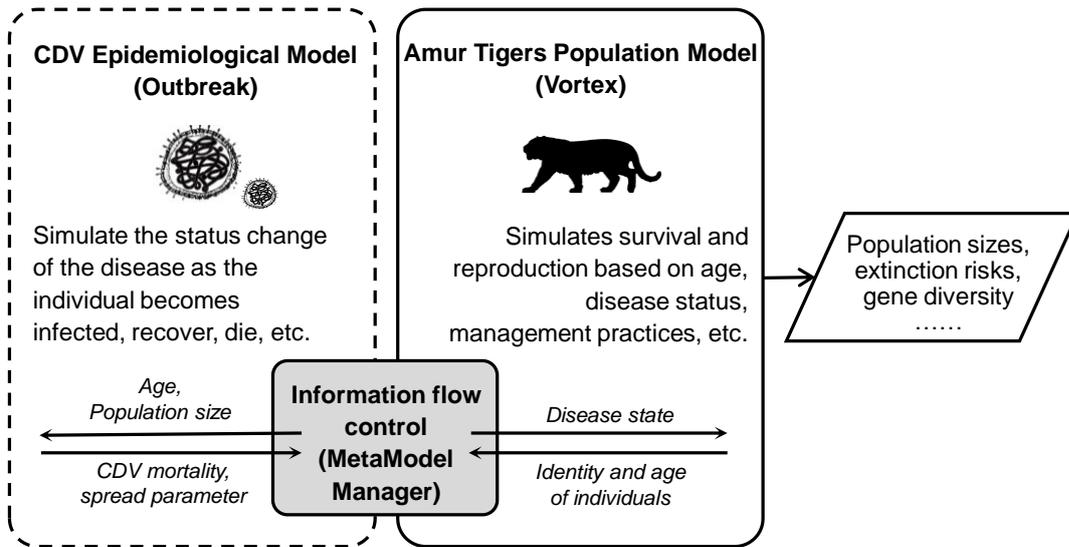
649 **Figure 2.** Schematic flowchart of the Amur tiger-CDV metamodel structure used for this

650 analysis. The PVA program acts as the system model (solid outline) to simulate individual

651 survival and reproduction based on individual and population state variables (shown in italics)

652 passed from other models. Epidemiological model (dashed outlines) simulates individual

653 transitions in disease status. The central information flow control program passes state

654 variables between the system and modifier models at appropriate time steps. Rounded

655 rectangles represent software components, and parallelograms identify model output

656 variables from Vortex.

657
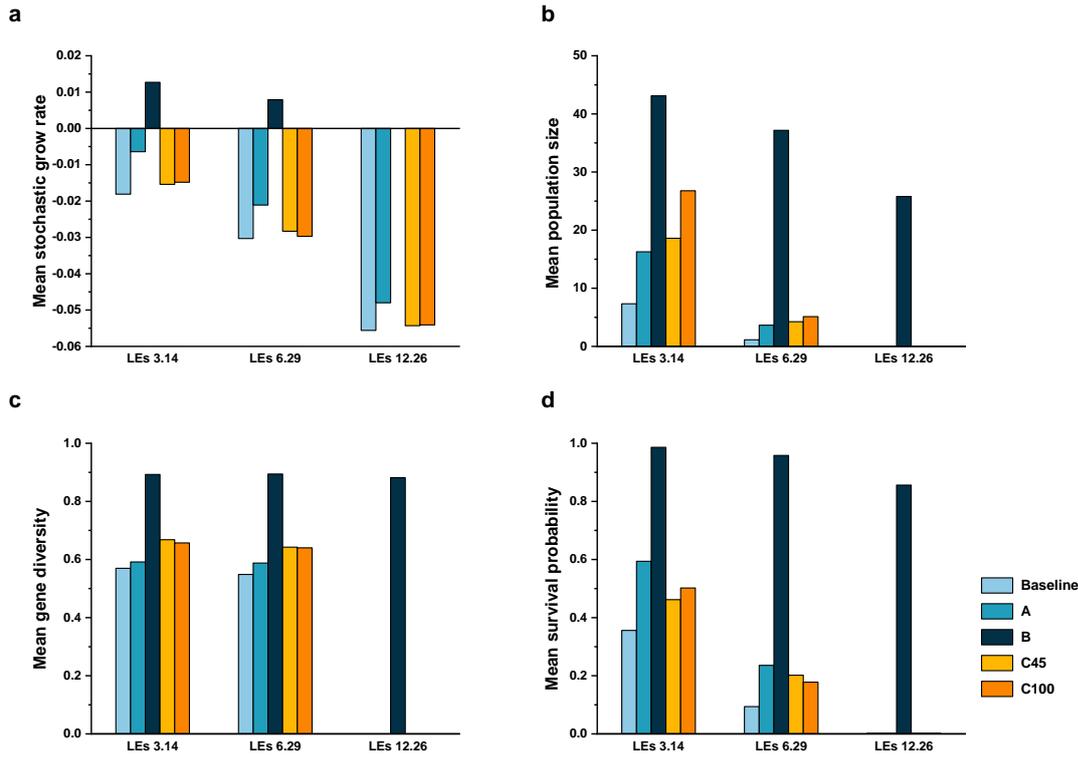
Figure 3. Estimates of stochastic population growth (a), population size (b), genetic diversity (c) and survival probability (d) for the small Amur tiger population under different management alternatives and lethal equivalents (LEs) over 100 years based on the average of 500 model runs. Scenario A: 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.

665
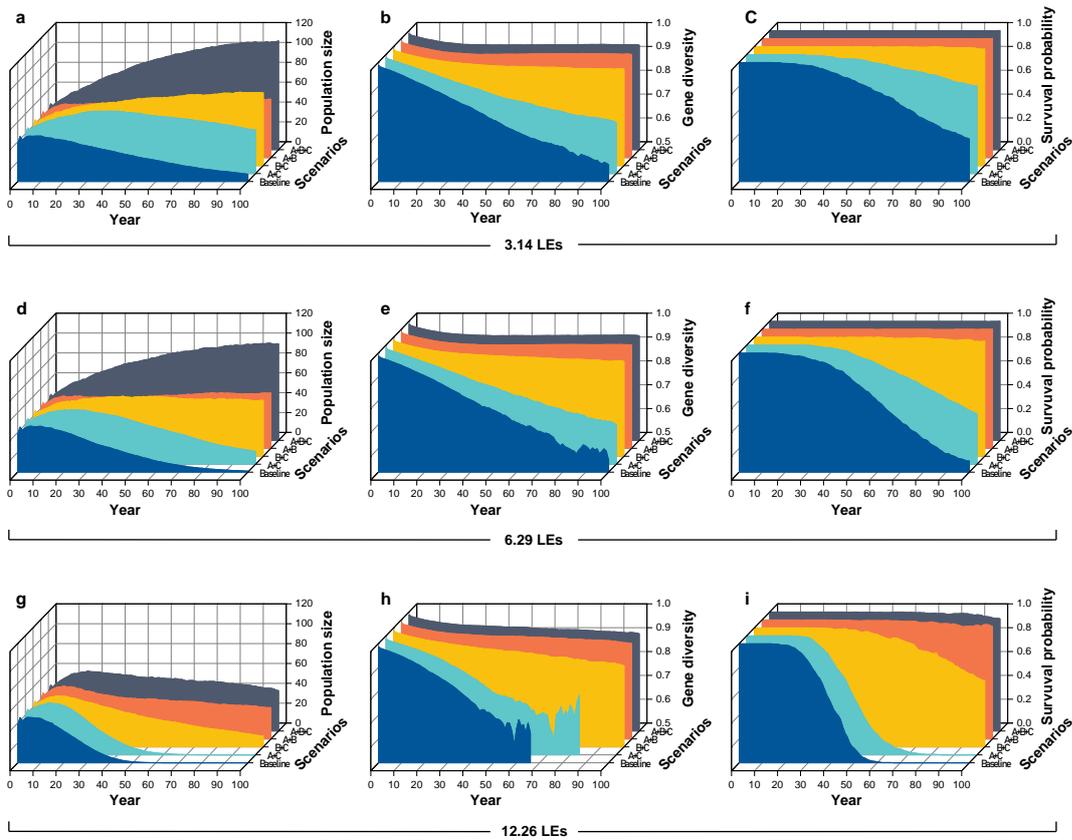
Figure 4. Changes in population size, genetic diversity, and survival probability of small

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.

671