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Viability analysis of the wild sika deer (*Cervus nippon*) population in China: Threats of habitat loss and effectiveness of management interventions

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ABSTRACT

Wild sika deer (*Cervus nippon*) are threatened by habitat loss and fragmentation throughout East China. Using 18-year demographic data, we conducted a viability analysis to predict the fate of a wild sika deer population threatened by loss of suitable habitat in the Taohongling National Nature Reserve, Southeast China. We simulated performance of proposed management interventions — population recruitment and habitat restoration — in preventing the sika deer population from declining. In the scenario where 60% or 30% of suitable habitat was lost, the population viability model predicted 99.6% and 85.5% probability of population decline by 40 years, respectively. The modelling demonstrated that carrying capacity, which was affected by vegetation succession and socioeconomic development, would restrict the growth of the sika deer population. The survival rate of adults is the element most affecting population growth, yet supplementation of adult deer was predicted to be less effective than habitat restoration in reducing risk of population decline in all habitat scenarios. Large-area but less-intensive restoration should be considered at initial stage of the intervention if the funding was sufficient to support. Regarding these findings, we recommend future management interventions to target towards increasing suitable habitat as well as preventing habitat loss and fragmentation in Taohongling National Nature Reserve. The zoning scheme and its management need to be regulated with conservation incentives.

1. Introduction

Large ungulates are a mammal group of both economic and ecological importance by supplying goods to human societies and contributing to ecological processes at both local and regional levels (Hobbs, 1996). The absence of large ungulates can have serious impacts on processes of vegetation successions, disrupts the stability of ecological interactions (Gray, Phan, Pin, & Prum, 2012) and shifts in the species abundance throughout the food chain (Pringle, Young, Rubenstein, & McCauley, 2007). Accordingly, managment effort is needed to prevent the consequences of unforeseen declines or extirpations of large ungulates cascading through entire ecosystems (Dirzo et al., 2014). Currently, the main threats that induce population decline and extinction of large ungulates are over-exploitation and habitat loss (Mysterud, 2011; Naranjo & Bodmer, 2007). Over-exploitation impedes persistence of ungulates which leads to substantial declines and changes in the demographic structure of their populations (Milner, Nilsen, & Andreassen, 2007; Mysterud, 2011; Setsaas, Holmern, Mwakalebe, Stokke, & Røskaft, 2007). Habitat loss intensifies i) inter- and intra-specific competition for resources, ii) individual stress levels, and iii) risk of human-ungulate conflicts (Western, Russell, & Cuthill, 2009). The combined effect of these two risk factors is subsequently anticipated to compromise the long-term viability of affected populations. In this context, the absence of effective conservation planning and management could have catastrophic consequences on wild ungulate populations: estimates from Hoffmann et al. (2015) indicate that the abundance of world's ungulates would have plunged to one eighth of current numbers in the absence of conservation actions over the past two decades. Since the magnitude and type of risk factors vary across a species' range, it is critical to design actions tailored to reduce context-specific pressures for long-term survival of ungulate populations in the wild.

Population Viability Analysis (PVA) is instrumental to inform conservation and management of threatened species under uncertainty (Akçakaya & Sjögren-Gulve, 2000; Possingham, Lindenmayer, & Norton, 1993). PVA is broadly used as a predictive tool to estimate a population's (or species') risk of extinction through stochastic simulations of demographic and life-history parameters in different scenarios

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(Beissinger & Westphal, 1998; Reed et al., 2002). PVAs have been used for evaluating the consequences of multiple risk factors on the persistence of wildlife populations such as the effects of cougar (*Puma concolor*) predation on big horn sheep (*Ovis canadensis*; Festa-Bianchet, Coulson, Gaillard, Hogg, & Pelletier, 2006), habitat fragmentation on viability of Przewalski's gazelle (*Procapra przewalskii*, Hu, Jiang, & Mallon, 2013), as well as the consequences of hurricanes on the extinction risk of an isolated howler monkey (*Alouatta palliata* mexicana) population (Ameca y Juárez, Ellis, & Rodríguez-Luna, 2015). Furthermore, PVAs have been used to explore how different regimes of habitat restoration and enlargement of protected areas would benefit populations of threatened amphibians and birds (Di Minin & Griffiths, 2011; Perkins, Vickery, & Shriver, 2008). Although PVA has a prevalent position in conservation, there have been restrictions on its applications due to the factors affecting PVA models' ability of generating accurate and precise predictions, such as data quality, parameter estimation and model validation (Reed et al., 2002). Especially for endangered species, few studies could provide adequate data of population viability for estimating parameters required by PVA (Beissinger & McCullough, 2002). Nevertheless, it is possible to supplement demographic and life history data for a population of concern by information from another well-monitored population that is of the same or a closely related species (Tian et al., 2011; Zambrano, Vega, Herrera M., Prado, & Reynoso, 2007). In this study, we applied a PVA modelling framework to estimate the effectiveness of conservation actions for an endangered ungulate species in China - sika deer (*Cervus nippon*), whose wild populations are greatly depleted in most of its historical distribution (Jiang, Kaji, & Ping, 2015).

Sika deer is endemic to Asia, with wild populations widely distributed from East to South China in the mid-19th century. However, through the 20th century, hunting and habitat loss caused severe declines and extinction of most of the sika deer populations across its historical range (Guo & Zheng, 1999). To prevent the species from extinction, hunting sika deer has been banned since 1988 in China (NPC, 1988) and all wild populations have been protected by law since 1989 (SFA & MOA, 1989). From 1965 to 2001, 17 nature reserves were established across the country to protect remaining wild populations of sika deer and their habitats (McCullough, Jiang, & Li, 2009). The latest nationwide Terrestrial Vertebrate Survey of China (SFA, 2008) suggested that banning hunting and establishment of nature reserves helped total number of wild sika deer to increase from ~1500 individuals in the early 1980s to ~8500. Despite the remarkable growth of wild populations, genetic diversity of the sika deer in China is relatively low compared with wild populations in Japan (Lü, Wei, Li, Yang, & Liu, 2006,). Two small, isolated populations in Southeast China were identified as showing strong genetic differentiations from the majority wild populations (Wu, Hu, Fang, Kong, & Jia, 2006; Wu, Wan, & Fang, 2004), and thus merit special conservation efforts for maintaining genetic diversity of sika deer in China (McCullough, Jiang et al., 2009). Focusing on one of the populations, we studied the sika deer in Taohongling National Nature Reserve (hereafter referred to as TNNR). From 1987 to 1998, the TNNR population increased at an average rate of 17 individuals per year (The administration of TNNR, 1990; Xu, Lu, Sheng, & Gu, 1998). However, the rate then decreased to 4 individuals per year, with which the population size reached ~365 individuals by 2011 (Jiang, Xu, Liu, & Zhou, 2012). Empirical and theoretical estimates have showed that thousands of individuals are required for a population to be able to cope with demographic and environmental stochasticity, catastrophic events, and ensure its long term survival (Traill, Brook, Frankham, & Bradshaw, 2010). Aiming for the maintenance of self-sustaining deer populations, a variety of conservation actions have been attempted, including habitat improvement (Bergman, Bishop, Freddy, White, & Doherty, 2014; Genghini & Capizzi, 2005), reintroductions (Bar-David, Saltz, Dayan, Perelberg, & Dolev, 2005; Jiang et al., 2000), and implementing bans on hunting and trade of deer body parts (Yang, Meng, Xia, & Feng, 2003). In TNNR, potential threats on population growth were reported to be traps and degradation of suitable habitat (Wu, 2008; Li, Wang, & Shi, 2010). To address these issues, we propose two management interventions: i) habitat restoration aiming to improve quality of the remaining habitat by shifting vegetation structure towards that appropriate for sika deer, and increasing connectivity among the fragmented habitats; and, ii) increase population abundance by sustainably supplementing the TNNR population with captive-raised deer. Since the funding is insufficient for implementing both interventions, which is a common situation in conservation practice, it is imperative to justify conservation investments based on identification of the option with the greatest efficiency.

In this study, making use of an 18-year life table from a well-monitored sika deer population in China, we built a PVA modelling framework for the sika deer population in TNNR, aiming to: i) estimate the risk of population decline and extinction within 40 years in three contrasting scenarios of suitable habitat availability (one constant and two decreasing trends); and, ii) explore performance of two management options (habitat restoration and population supplementation) in preventing population decline in different scenarios.

2. Materials and methods

2.1. Study area

The TNNR (29°42′–29°53′N, 116°32′–116°43′E) is a National Reserve of ~125 km^2. Required by regulations on natural forest preservation (SFA, 1998), the management authority of TNNR has banned logging and firewood collection since the late 1990s. Wild fires have been also strictly monitored and prevented for the same reason. Following the "Man and the Biosphere" reserve model of UNESCO (Batisse, 1982), TNNR is composed of a core zone (26.7 km^2), a buffer zone (18.3 km^2) and an experimental zone (80 km^2). Settlements of local residents were moved out of the core zone to prohibit the impact of human activities on wildlife and its habitat. During the past three decades, vegetation of TNNR changed due to the policies of forest protection. The logging ban and stringent fire control has facilitated a fast succession of vegetation as well as a rapid growth of abandoned timber trees. Consequently, substantial suitable habitat for sika deer–characterized by open shrub lands and grasslands - was replaced by evergreen broadleaf and coniferous forest (Fu et al., 2006; Liu, X, Jiang, & Wu, 2009; Fig. S1). Moreover, owing to local economic development and urbanization, large areas of suitable habitat in the experimental zone have been lost (Fig. S2, Wu, 2008; Li, Li, Miao, Xie, & Yuan, 2014).

2.2. Model structure and parameters

Inferences of vital rates from large, increasing, or healthy populations may not be applicable to those populations that are small, declining, or endangered (Johnson, Mills, Stephenson, & Wehausen, 2010). In this study, we parameterized our models with vital rates obtained from an 18-year life table which was constructed by conducting a capture-mark-recapture method to 111 annually-monitored sika deer in Tiebu Nature Reserve in West China from 1987 to 2004 (Guo & Zheng, 2005, Table S1). During this period, the Tiebu population showed a slow-growing trend similar to what was observed for the TNNR population, and it was inferred to reach the carrying capacity of the reserve in 2005 (Guo & Zheng, 2005; Guo, 2002). Tiebu Nature Reserve was furthermore reported to be undergoing a decrease in habitat suitability for sika deer caused by human disturbance such as road construction and expansion of residential areas (Zhao et al., 2014). Referring to these shared risk factors, vital rates of the Tiebu population are qualified for parameterizing PVA models of the TNNR population.

The finite population growth rate (λ) estimated from the time series data of the Tiebu population was 1.032 (Guo & Zheng, 2005). We estimated demographic parameters separately for males and females due to the existing skewed sex ratio (approximately 1 male: 3 females) and sex-specific mortality rates (Guo & Zheng, 2005). Breeding system of sika deer was modelled as polygynous, because adult males mate with several females during the rut (Davies, 1991). We adopted five age stages – fawns, yearlings, juveniles, adults, and senescent – based on tooth eruption-wear patterns (Guo & Zheng, 2005). Fertility was expressed in terms of the proportion of female and male offspring to all sexually mature females. Because the observed sex-ratio of new-borns in sika deer population is close to 1: 1 (Guo & Zheng, 2005; Ohnishi et al., 2009; Suzuki, Koizumi, & Kobayashi, 1992), we estimated the ratio of female to male fawns per hind as one for each stage class. The dynamics of the population were modelled from time *t* to *t + 1* using age stage- and sex-structured matrices (Akçakaya & Root, 2013). The matrices parameterized with vital rates from the period 1987–2004 are:

		♀					♂		
0	0	F_j	F_a	F_s	0	0	0	0	0
S_y	0	0	0	0	S_y	0	0	0	0
0	S_j	0	0	0	0	S_j	0	0	0
0	0	T_a	S_a	0	0	0	T_a	S_a	0

F_j, F_a,
F_s,
S_f

m_x
S_f
m_x
Akçakaya and Root, 2013
Akçakaya & Root, 2013
S_y
–
S_j
–
S_a
–
S_s
T_a
T_s
McCullough, Jiang et al., 2009
λ
N_t

N_t
λ
Guo and Zheng, 2005
Guo & Zheng, 2005

Sika deer populations are characterized by a high intrinsic rate of increase and no significant density-dependent effect on population growth before population crash (Matsuda, Kaji, Uno, Hirakawa, & Saitoh, 1999). For certain sika deer populations, density-dependent mortality did not take place until carrying capacity (*K*) was reached (Kaji, Koizumi, & Ohtaishi, 1988), and there was no evidence that the population growth could be impeded by very small population size (Kaji, Okada, Yamanaka, Matsuda, & Yabe, 2004; Matsuda et al., 2002). *K* is defined as the upper limit of population abundance per unit of area, above which the population fluctuates and tends to decline (Akçakaya & Root, 2013). An indirect measure of *K* is the maximum number of individuals that an area can support given the food, habitat, water, and other vital resources available (Lande, 1993). In this study, *K* was estimated as the number of deer individuals that suitable habitat in the TNNR can support. Li et al. (2014) assessed habitat suitability for TNNR based on habitat selection of sika deer as well as abiotic, biotic and anthropogenic characteristics of the reserve. Potential suitable habitat was estimated to be ~18.3 km^2, without taking into account anthropogenic impacts such as residential area and roads; suitable habitat was estimated to be ~33.88 km^2 by excluding unsuitable habitat due to anthropogenic impacts (Fig. S2). The minimum mean home range size of sika deer was estimated between 0.07–0.11 km^2 by radio-collaring deer all year round in Tanzawa Mountains 20 km of Tokyo Metropolis, Japan, where the sika deer are under human disturbance (Borkowski & Furubayashi, 1998). Based on the area of suitable habitat and minimum home range of individual sika deer, *K* of the TNNR deer was estimated to be 368 ± 105 individuals (Li et al., 2014). Spatial heterogeneity can result in an apparently broad range of *K* values over sika deer habitats (1.34–98.4 deer/km^2, Iijima & Ueno, 2016). Besides, socioeconomic differences between regions could also impact on habitat quality and availability, and so drive discrepancies in *K* (Jiang et al., 2015). Considering the reported threats on TNNR habitat and their possible impact on carrying capacity, we adopted the estimate of *K* from Li et al. (2014) in our models, despite it is low when compared with data from some studies on sika deer in Japan (e.g. 118 deer/km^2, Kaji et al., 2004). Density dependence was modelled with a ceiling effect. Under this type of density dependence, the population is assumed to grow until it reaches the carrying capacity of the habitat, then population size is expected to fluctuate randomly around this threshold (Lande, 1993).

2.3. Incorporating stochasticity in population projections

Demographic changes of sika deer in TNNR were projected using a stage-structured stochastic model implemented in RAMAS Metapop version 6.0 (Akçakaya & Root, 2013). RAMAS Metapop is a simulation package for predicting population trends which has proven to be robust provided that input parameters derived from empirical data and the biology of the species is well-known (Akçakaya & Sjögren-Gulve, 2000; Akçakaya, Franklin, Syphard, & Stephenson, 2005; Brook et al., 2000). Although the demography of the sika deer in TNNR has not been comprehensively studied, the demographic data derived from the Tiebu population makes it possible to estimate the future trends of the TNNR population via PVA modelling. To quantify short-term effects of immediate risk factors, we tracked processes annually for 40 years. For each model we ran 1000 replications, which is standard for determining risk curves with precision (Akçakaya & Root, 2013). Demographic stochasticity of the population was incorporated by sampling the number of survivors from a binomial distribution, and number of offspring from a Poisson distribution (Akçakaya & Root, 2013).

The impact of environmental stochasticity on the sika deer population was modelled by randomly selecting values from normal distributions described by a standard deviation matrix of the vital rates (fertility and survival rates) which were structured identical to the stage matrix, and random fluctuations within the estimated standard deviation of *K* (Akçakaya, 2000). Wild fires were assumed to be catastrophic events affecting *K* of the TNNR by changing habitat quality for sika deer. However, we did not include possible impact of wild fires in our model, because the frequency of fires in TNNR has been zero since 2001 due to strict fireproof actions. Such a strong policy interference prevents a sound estimation on fire frequency.

We used the average population size (N = 330) observed in surveys on sika deer between 1998 and 2011 (Jiang et al., 2012; Jiang, 2009; Xu et al., 1998) as the initial population size for each modelled scenarios (see below). Population decline was defined as the abundance falling below the initial size by the end of 40-year time period. Likewise, population extinction was assumed to take place when only one individual was left at any time within this time period.

2.4. Sensitivity analysis and management scenarios

Sensitivity analysis was used in combination with the PVA to evaluate the importance of model parameters and identify those which may have a greater influence in model outcomes with variations from baseline values (Morris & Doak, 2002). In doing so, we changed the value of each parameter of the PVA model by ± 10%, while holding all other parameters constant (Di Minin & Griffiths, 2011; Ameca y Juárez et al., 2015). The sensitivity analysis was implemented in a baseline scenario of no decrease in K nor management interventions. Model parameters selected for sensitivity analysis were survival rates of all age stages and fecundity.

We simulated two management interventions, namely, habitat restoration and population supplementation. Habitat restoration was simulated by increasing suitable habitat which was reflected as the increase of K in the model. Population supplementation was simulated by introducing sika deer to the TNNR population at fixed time intervals. Each intervention was modelled in three assumed habitat scenarios referring to the documented situation of the TNNR (Liu, 2007; Wu, 2008; Li et al., 2014): one neutral scenario where the loss of suitable habitat is stopped, and two negative scenarios with yearly gradual loss of suitable habitat by 30% and 60% (~10 km^2 and ~20 km^2, respectively) for 40 years.

The assessment of habitat suitability showed that suitable habitat was fragmented by farmlands and roads in the Litouling, Dashenshan, and Shangbaishu areas in southern and eastern TNNR (Fig. S2). If habitat loss was stopped and habitat connectivity was increased in these areas, the amount of suitable habitat could increase ~30% (Li et al., 2014). We designed two forms of habitat restoration that would increase K by 30%: i) annually increasing 0.75% of the initial K for 40 years (management R1); and, ii) increasing 30% of initial K in the first year of the 40-year time window (management R2). We did not model restoration of the entire potential suitable habitat in TNNR, considering that such a scale of management will be unlikely to be funded in a foreseeable future.

We simulated population supplementation by adding 11 adult individuals (3 males and 8 females) every 4 years to the TNNR population until year 40, making a total of 110 introduced deer (management I1). To evaluate how a more intense supplementation influences risk of population decline, we simulated introducing 22 adult individuals (6 males and 16 females) every 4 years until year 20, which also summed up to 110 introduced deer (management I2). The number of supplemented individuals was roughly equal to the increased K for modelling habitat restoration, so as to make results of two management interventions comparable. Because the genetic structure of the TNNR population is different from most captive deer in China, the source of supplementation is planned to be a captive-raised sika deer population bred by rescued individuals from the TNNR population itself. We simulated the introduction of male and female deer with the sex ratio of 1 male: 3 females (the ratio we used to parameterize the model). Such a decision was also assumed to be likely to facilitate successful reproduction in an early stage, since males would potentially have to compete with established males during the rut. Despite being more effective in increasing new-borns for the receiving population, introducing only females was not adopted for modelling, as it is not practical for keeping sustainable supplementations from a relatively small source population.

3. Results

3.1. Probability of population extinction and decline by 40 years

Our analyses showed that the probability of population extinction was not predicted to be higher than 20% until K decreased by 80% (Fig. 1a). Nevertheless, by simulating population trajectories in different magnitudes of decline of suitable habitat, we found that

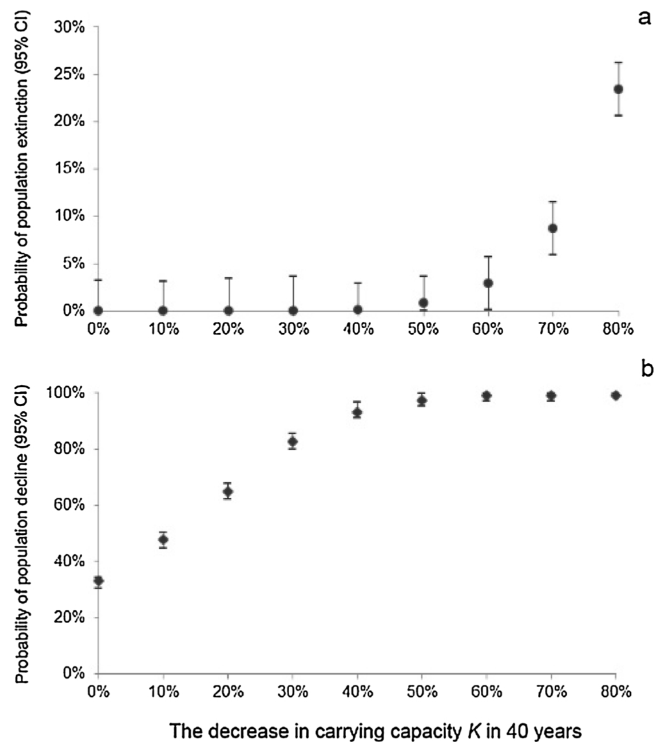

Fig. 1. Potential impacts of decreases in carrying capacity (K) on probabilities of population extinction (panel "a") and population decline (panel "b") by 40 years for the sika deer (*Cervus nippon*) in Taohongling National Nature Reserve, China. Probabilities of population extinction and decline are given with 95% confidence intervals. Population decline is defined as the population decreasing below the initial population size of the model (n = 330).

probabilities of population declining below the initial size benchmark would be over 50% if K decreased by 10%, and risk of decline was estimated to be over 90% when the decline in K was greater than 40% (Fig. 1b).

3.2. Sensitivity analysis

Results of sensitivity analysis (Table 1) showed that the survival rate of adults was the parameter most affecting the growth rate (λ) of the TNNR sika deer population, followed by the survival rate of fawns. Increment of ± 10% in the survival rate of adults resulted in ± 5% variations of λ which were nearly five times higher than the variations generated by changing ± 10% the baseline values of other parameters. The sensitivity analysis also indicated that the survival rate of adults had the strongest influence on risk of population decline, while predicted risks of population extinction were zero and not sensitive to any parameters.

3.3. Performance of habitat restoration

We evaluated the performance of habitat restoration (management R1, R2) by comparing it with results of no management actions modelling across three assumed scenarios, focusing only on mitigating risk of population decline. We did not evaluate its performance on risk of population extinction, as it was predicted to be lower than 10% in any scenario by the end of 40 years (Fig. 1). In the neutral scenario, the restoration form of increasing K at a rate of 0.75% per year (management R1) reduced the probability of population decline from 19% to 14% by 10 years, and from 33% to 8% by 40 years, whereas restoration implying a 30% increase of K in year one (management R2) reduced the probability of decline from 33% to 2% by 40 years (Fig. 2a). In the negative scenario "A" (30% loss of suitable habitat), the probability of

Table 1
Sensitivity analysis of model parameters used to estimate probabilities of population decline and population extinction for sika deer (*Cervus nippon*) in the Taohongling National Nature Reserve, China.

	Probability of decline (95% CI)	Probability of extinction (95% CI)	λ
10% increase in parameters			
Fawn survival	0.1800 (0.1520–0.2080)	0	1.047
Yearling survival	0.2150 (0.1870–0.2430)	0	1.047
Juvenile survival	0.2030 (0.1750–0.2310)	0	1.044
Transition to adult	0.2020 (0.1740–0.2300)	0	1.0447
Transition to senescent	0.3160 (0.2880–0.3440)	0	1.0365
Adult survival	**0.1020 (0.0740–0.1300)**	0	**1.0904**
Senescence survival	0.3410 (0.3130–0.3690)	0	1.0368
Adult fecundity	0.1940 (0.1660–0.2220)	0	1.0462
Senescence fecundity	0.2820 (0.2540–0.3100)	0	1.0365
10% decrease in parameters			
Fawn survival	0.5090 (0.4810–0.5370)	0	1.020
Yearling survival	0.5090 (0.4810–0.5370)	0	1.0238
Juvenile survival	0.5030 (0.4750–0.5310)	0	1.0238
Transition to adult	0.4930 (0.4650–0.5210)	0	1.0238
Transition to senescent	0.3170 (0.2890–0.3450)	0.0010 (0.0000-0.0290)	1.0349
Adult survival	**0.9480 (0.9200–0.9760)**	0	**0.9825**
Senescence survival	0.3310 (0.3030–0.3590)	0	1.0349
Adult fecundity	0.5310 (0.5030–0.5590)	0	1.0238
Senescence fecundity	0.3510 (0.3230–0.3790)	0	1.0342
Parameters constant	0.3310 (0.2730–0.3290)	0	1.0357

Model parameters are increased and decreased by 10% of their baseline estimates while holding all other parameters constant, to identify the parameter most impacting probabilities of population decline and extinction. The last row shows the probabilities when all vital rates are of constant values of baseline estimates. Parameters causing the greatest effect on λ are highlighted in bold. The benchmark of population decline corresponds with the initial population size of the model (n = 330). Population extinction is estimated to hit when population abundance reaches one individual.

population decline was predicted to be 85% by 40 years in absence of management interventions. When management took the form of a small yearly increase in *K* (management R1), the probability of decline decreased to 37% by 40 years, and to 22% when *K* was increased by 30% at once (management R2, Fig. 2c). Not surprisingly, the highest probability of population decline was predicted in the scenario with the greatest loss of suitable habitat: in absence of management interventions, losing 60% of suitable habitat (negative scenario B) would induce population decline by 40 years in nearly 100% of the cases (Table 2). In this scenario, the small yearly increase in *K* reduced the probability of decline to 89.5%, while the increasing *K* by 30% at once resulted in a probability of 78% (Fig. 2e).

3.4. Performance of population supplementation

Because population growth rate λ is highly sensitive to the survival rate of adults, we simulated the introduction of individual adults to the TNNR population with two forms of supplementation intervention. In the neutral scenario, population supplementation of introducing 11 individuals every 4 years (management I1) reduced the probability of decline from 33% to 21% by 40 years (Fig. 2b). This action performed better than introducing 22 individuals every 4 years within the first 20 years (management I2) which did not change the probability of decline significantly, compared with a non-management scenario ($t = 1.089$, $P > 0.05$, Table 3). Examination of the two negative scenarios revealed that the probability of decline increased despite population supplementation being implemented. When 30% of suitable habitat was lost (negative scenario A), the introduction of 11 individuals every 4 years brought a significant reduction of the probability of decline ($t = 3.217$, $P < 0.05$, Table 3), but a more intense supplementation within the first 20 years did not cause any significant change ($t = 1.089$, $P > 0.05$, Fig. 2d, Table 3). In negative scenario B, neither management I1 nor management I2 substantially lowered down the probability of population decline within the 40-year time window assessed (Fig. 2f, Table 3).

4. Discussion

4.1. Habitat and population dynamics of sika deer

Habitat quantity and quality are elements affecting population dynamics of a given species, with strong influence on small and isolated populations (Stevens & Baguette, 2008). Studies found that movements of roe deer (*Capreolus capreolus*) among habitats were markedly influenced by habitat quality (Pettorelli et al., 2003), and increased environmental productivity could increase roe deer abundance (Melis et al., 2009). Home ranges of moose (*Alces alces*) were found to be larger if they had high cover of unproductive habitat types, while smaller home ranges contained higher proportions of habitat with sufficient food and cover (Bjørneraas et al., 2012). In TNNR, vegetation succession and increased habitat loss influence habitat conditions and hence the resident sika deer population. Vegetation succession in the core zone and buffer zone is attributed to a complete elimination of human activities and wild fires. Without conservation interventions, evergreen broadleaf forest and coniferous forest may keep growing as the vegetation succession continues, causing a further decline of suitable habitat in TNNR. On the other hand, human encroachment keeps shrinking and fragmenting suitable habitat in the experimental zone. As management authorities of nature reserves in China are not empowered to punish individuals or organizations for conducting prohibited activities in the reserve, the zoning scheme of TNNR is ineffective to control impacts of socioeconomic development on sika deer's habitat, especially in the experimental zone which is inhabited by over 20,000 residents (Li et al., 2014; Liu & Yu, 2010; Wu, 2008). Our predictions on population trajectories of the TNNR sika deer indicated that a low to moderate magnitude of decrease in *K* would raise risk of population decline from 33% to 85% and 99.8% by 40 years, respectively, calling for actions targeting improvements to the habitat condition.

For long-lived vertebrates with relatively low mortality, delayed maturity, low fecundity and iteropary, the survival rate of adults is the most influential vital rate of population growth (Heppell, Caswell, & Crowder, 2000; Read & Harvey, 1989). Results of sensitivity analysis of our study followed this general condition of large-sized mammals. In TNNR, the adult survival of sika deer is threatened by hunting devices such as electricity nets and snare traps (Li et al., 2010). These devices, low-cost and easy to make, are widely used to prevent wild boars from entering farmlands and are also placed in and around the reserve. In recent years, sika deer have increasingly appeared in the experimental zone and outside the reserve where hunting traps are placed, and the number of injured individuals has also increased (Li et al., 2013; Wu, 2008). Injured deer have little chance of surviving without rescue from human. To reduce the threat, environmental friendly programs need be designed and implemented for controlling the impact of wild boars with support and participation of the residents living in the TNNR.

4.2. Management interventions

Modelling results showed that performance of two management intervention forms related to habitat restoration — yearly small and one early large intervention—varied across different regimes of habitat loss. Compared with restoring a small amount of potential suitable habitat every year, restoring targeted habitat in one single early

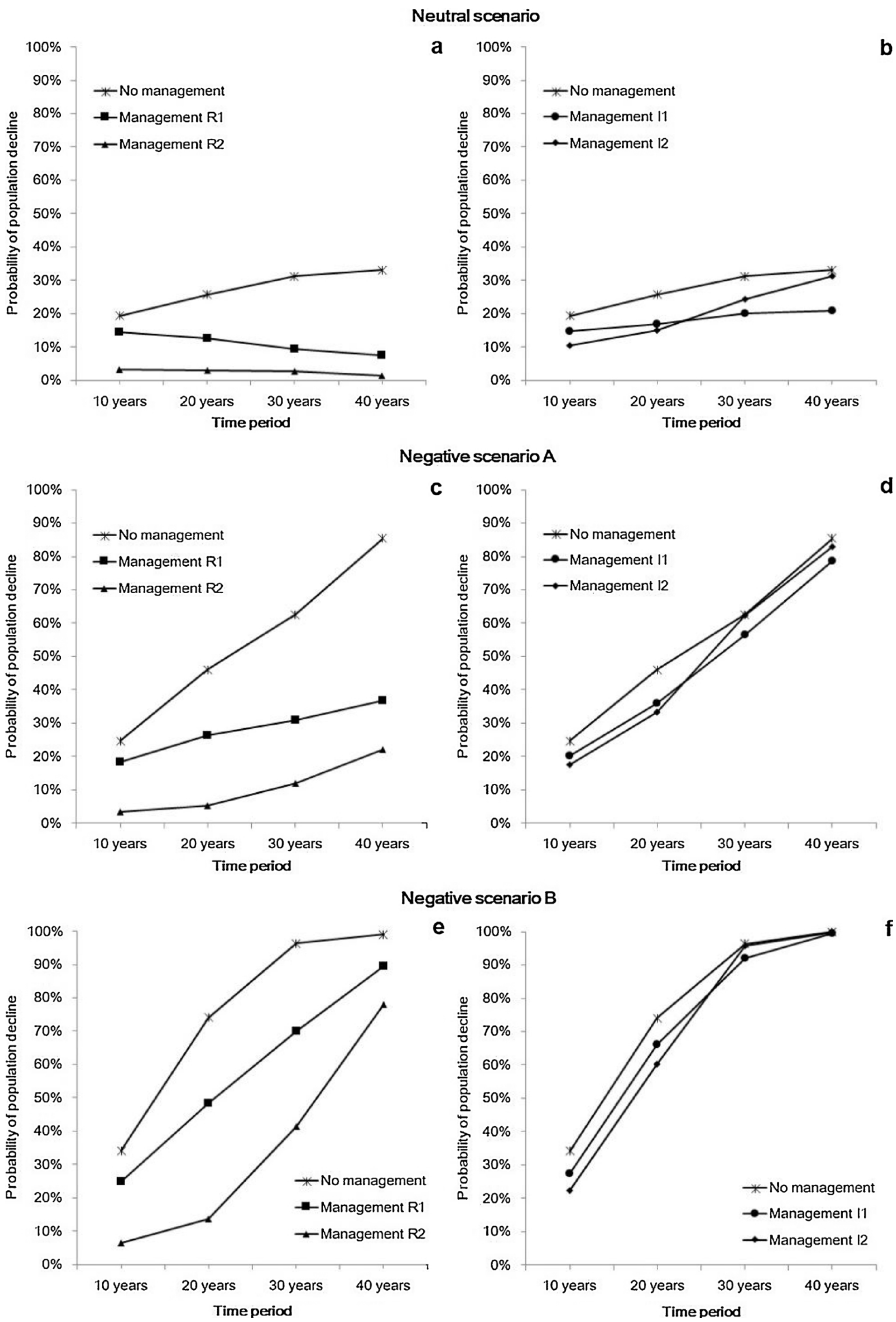

Fig. 2. Probabilites of population decline for the sika deer (*Cervus nippon*) of Taohongling National Nature Reserve, China under different management interventions implemented in three habitat scenarios. Panels give decadal estimates for different modelled conditions: panels "a", "c", and "e" show the contributions of no management, management R1 (increasing *K* by 0.75% per year), and management R2 (increasing *K* by 30% at once); panels "b", "c", "f" show the contributions of no management, management I1 (introducing 11 individual adults every 4 years for 40 years), and management I2 (introducing 22 individual adults every 4 years for the first 20 years), respectively. In neutral scenario, we simulated no loss of suitable habitat. In two negative scenarios, we simulated a yearly gradual loss of suitable habitat that caused 30% (negative scenario A) and 60% (negative scenario B) decrese in *K* in 40 years. Population decline is defined as the population decreasing below the initial population size of the model (n = 330).

intervention and ensuring maintenance of the habitat would significantly reduce the probability of population decline throughout the 40-year time window assessed (Table 2).

Focusing on the population supplementation strategy, our results indicated that an introduction of equal number of deer implemented within 40 years was better than that implemented within 20 years in the neutral scenario (constant suitable habitat) and negative scenario A (suitable habitat decreased by 30%, Table 2). Nevertheless, the performance of both options were not significantly different in negative scenario B ($t = 0.198$, $P > 0.05$, Table 3).

In all three habitat scenarios, habitat restoration was predicted to be more efficient for minimizing the risk of population decline than population supplementation (Table 2). The modelling results inferred that supplementing individual adults reduced the probability of population decline, yet its effect would not be lasting due to limited suitable habitat. Different from population supplementation, restoring suitable habitat and hence increasing *K*, would bring a greater chance for long-standing population growth. Habitat restoration also holds great importance to the TNNR population for the little feasibility of increasing the connectivity with other sika deer populations, since the closest neighbouring sika population is 350 km away and was suggested to be managed as an independent unit due to its strong genetic differentiation (Wu et al., 2004). Therefore, conservation actions are recommended towards maintaining current suitable habitat for sika deer, and implementing interventions to increase the carrying capacity.

To prevent further declines in suitable habitat, more effort is needed

Table 2
Probability of population decline of sika deer (*Cervus Nippon*) under management interventions in three habitat scenarios in the Taohongling National Nature Reserve, China.

Neutral Scenario		
	Probability of decline (%)	Confidence Interval (%)
No management	33.2	**30.4–36**
Management R1	7.5	4.7–10.3
Management R2	1.5	0–4.3
Management I1	21.0	18.2–23.8
Management I2	31.0	**28.2–33.8**
Negative Scenario A		
	Probability of decline	Confidence Interval
No management	85.1	**82.3–87.9**
Management R1	36.6	33.8–39.4
Management R2	22.1	19.3–24.9
Management I1	78.6	**75.8–81.4**
Management I2	82.9	**80.1–85.7**
Negative Scenario B		
	Probability of decline	Confidence Interval
No management	99.8	**97–100**
Management R1	89.5	86.7–92.2
Management R2	77.9	75.1–80.7
Management I1	99.5	**96.7–100**
Management I2	99.9	**97.1–100**

Probability of population decline indicates the likelihood that abundance of the sika deer population declines below the initial population size (n = 330) at the end of 40 years. Non-overlapping confidence intervals show a significant difference between predicted probabilities; overlapping confidence intervals (highlighted in Bold) indicate a likely non-significant difference between probabilities, which needs further statistic testing (Knezevic, 2008). Results of tests see Table 3.

Table 3
Summary of *t*-tests on probabilities of population decline of sika deer (*Cervus nippon*) in the Taohongling National Nature reserve, China.

Neutral Scenario		
		Management I2
No Management		t = 1.089, *P* = 0.2764
Negative Scenario A		
	Management I1	Management I2
No Management	**t = 3.217, *P* = 0.0014**	t = 1.089, *P* = 0.2764
Management I1	–	**t = 2.15, *P* = 0.0318**
Negative Scenario B		
	Management I1	Management I2
No Management	t = 0.1485, *P* = 0.882	t = 0.0495, *P* = 0.9605
Management I1	–	t = 0.198, *P* = 0.8431

t (t-score) is the ratio between the difference between two groups and the difference within the groups. *P* (p-value) is the probability that the results from sample data occurred by chance. A $P \leq 0.05\%$ indicates a significant difference between two groups is valid (highlighted in Bold).

for efficient management of the experimental zone. Theoretically, zoning of nature reserves aims to manage multiple uses through delineation of spatial boundaries to distinguish areas with varying degrees of suitable human impacts. In this way, socioeconomic development pressures can be shifted to the experimental zone from areas of high conservation value (Eigenbrod et al., 2009). The experimental zone takes up to 64% of the TNNR. As an area bearing a high level of human impacts, its potential for conservation value needs to be assessed systematically and regularly, for adjusting the relationship between socioeconomic development and wildlife conservation. Further research should focus on evaluating cumulative impacts of local development on the environment of TNNR, so as to guide such activities being performed with considerations on both conservation and development needs. Actions on controlling urbanization and expansion of roads need to be strengthened to curb habitat loss in the experimental zone. Despite humans presenting a threat to sika deer habitat in TNNR, there is evidence that deer are capable of coexisting with human communities in many parts of the world (Kaji et al., 2004; Kilpatrick & LaBonte, 2003). That sika deer increasingly dispersing to the experimntal zone also indicates the potential of the species adapting to human activities and landuse change. Therefore, shifts in residents' attitude towards sustainable development is needed for ensuring the long-term viability of the sika deer population in TNNR. In this regard, the management authority of the reserve should engage more actively in boosting environmental education of local residents, and guide them to develop livelihoods that are less impactful or damaging on the environment and wildlife.

TNNR is located in East China where the primary landscape is highly transformed owing to a long history of human inhabitation and intensive agricultural activities. It is impossible to increase *K* through enlarging the reserve that is surrounded by residential areas and farmlands. Forest thinning is a practice providing diverse understory and overstory vegetation conditions, and contributed to a generally neutral to positive effect on diversity and abundance of mammals, birds and invertebrate communities (Kalies, Chambers, & Covington, 2010; Verschuyl, Riffell, Miller, & Wigley, 2011). Deer such as the mule deer (*Odocoileus hemionus*) and the moose (*Alces alces*) were found to respond positively to enhanced volume of herbs and shrubs as well as diversified composition and structure of vegetation resulting from thinning (Sullivan, Sullivan, Lindgren, & Ransome, 2007). Thus, thinning is suggested for increasing habitat suitability in TNNR rather than conducting a logging ban. To minimize influence on wildlife, the use of large machines needs to be avoided and herbicide must be forbidden during habitat restoration. Based on the results of our modelling, we also suggest to carry out restoration interventions less intensively but covering a larger area at each time.

The models built for this study contributed a general understanding of the likely trends of the sika deer population in TNNR in response to different management interventions. With the purpose of testing our PVA model more rigorously and guiding adaptive management with direct targets tied to population persistence, it is necessary to improve current understanding of both ecological and socioeconomic mechanisms underlying the studied system, which need to be identified from more empirical studies. Thus, efforts are required to conduct a long-term, and more frequent monitoring scheme on both sika deer population and habitat dynamics in TNNR. Such a scheme is suggested to combine population models with monitoring and management, for coordinating ecological analysis with decisions and interventions closely (Bakker & Doak, 2008). As *K* is one of the key factors in PVA modeling, the accuracy of estimation on *K* is needed to be improved by studying sika deer's home range size in TNNR, including variations of individual home range size and the extent of home range overlaps. Considering that natural catastrophic events might also increase the vulnerability of the population to ongoing habitat pressure, we additionally suggest to carry out surveys on sika deer habitat right after the occurrence of these events such as floods and earthquakes, in order to capture possible impacts of dramatic changes in *K* or sudden population die-offs (Ameca y Juárez, Mace, Cowlishaw, & Pettorelli, 2012). As genetic effects appear unlikely to affect population growth of ungulates in the short-term (Johnson, Mills, Wehausen, Stephenson, & Luikart, 2011), we did not specify the effect of inbreeding depression in the PVA model covering 40 years (5–6 sika deer generations, Mattioli, 2009) in this study. Nevertheless, recovery activities that minimize future losses of genetic variation are still recommended for long-term persistence of this isolated sika deer population. For the maintenance of genetic variation, it is advisable to supplement the population based on well-designed breeding programs, and/or translocate individuals between isolated populations within the same subspecies (Balakrishnan, Monfort, Gaur, Singh, & Sorenson, 2003). More research is also required to quantify inbreeding cost relative to population growth of the sika deer populations in China for effective management of this endangered species.

5. Conclusions

Over 50% of the nature reserves designed for protecting sika deer in China are located in regions with high human density (McCullough, Takatsuki, & Kaji, 2009. In such a situation, effectiveness of nature reserves are often limited despite of their protected status (Zhang, Luo, Mallon, Li, & Jiang, 2017). Wild sika deer populations in these reserves will probably face an even greater risk of decline triggered by in situ habitat pressures such as habitat loss, fragmentation and successional changes in vegetation. In the absence of adaptive management strategies, the threatened status of sika deer in China would be difficult to change. Our findings quantified threats that sika deer in TNNR would face, and facilitated a better understanding on the advantages and limitations of different management interventions to maintain sika deer populations in China. The study revealed that a rigid conservation management model could not benefit threatened populations under diverse pressures. We suggest policy makers and reserve managers allocate resources for adjusting the current approach, so as to i) increase suitable habitat for sika deer and hence the carrying capacity within limited available area, and ii) to manage local development activities based on systematic assessment of their medium to long term impacts.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.jnc.2018.02.014.

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