An assessment of South China tiger reintroduction potential in Hupingshan and Houhe National Nature Reserves, China

Yiyuan Qin, Philip J. Nyhus, Courtney L. Larson, Charles J.W. Carroll, Jeff Muntifering, Thomas D. Dahmer, Lu Jun, Ronald L. Tilson

*Environmental Studies Program, Colby College, Waterville, ME 04901, USA
†Yale School of Forestry and Environmental Studies, New Haven, CT, USA
‡Department of Conservation, Minnesota Zoo, 13000 Zoo Blvd., Apple Valley, MN 55124, USA
§National Wildlife Research and Development Center, State Forestry Administration, People’s Republic of China
¶Ecosystems, Ltd., Unit B13, 12/F Block 2, Yautong Ind. City, 17 KoFai Road, Yau Tong, Kowloon, Hong Kong
#National Wildlife Research and Development Center, State Forestry Administration, People’s Republic of China
$Minnesota Zoo Foundation, 13000 Zoo Blvd., Apple Valley, MN 55124, USA

**Corresponding author at: Environmental Studies Program, Colby College, 5358 Mayflower Hill, Waterville, ME 04901 USA. Tel.: +1 207 859 5358; fax: +1 207 859 5229.**

E-mail address: pjnyhus@colby.edu (P.J. Nyhus).

A R T I C L E   I N F O

Article history:
Received 11 June 2014
Received in revised form 20 October 2014
Accepted 28 October 2014

Keywords:
Panthera tigris amoyensis
Reintroduction
Restoration
Conservation
China
Habitat
Wild boar Sus scrofa
Sika deer Cervus nippon
GIS

A B S T R A C T

Human-caused biodiversity loss is a global problem, large carnivores are particularly threatened, and the tiger (Panthera tigris) is among the world’s most endangered large carnivores. The South China tiger (Panthera tigris amoyensis) is the most critically endangered tiger subspecies and is considered functionally extinct in the wild. The government of China has expressed its intent to reintroduce a small population of South China tigers into a portion of their historic range as part of a larger goal to recover wild tiger populations in China. This would be the world’s first major tiger reintroduction program. A free-ranging population of 15–20 tigers living in a minimum of 1000 km² of habitat was identified as a target. We assessed summer and winter habitat suitability of two critical prey species, wild boar (Sus scrofa) and Sika deer (Cervus nippon), using GIS spatial models to evaluate the potential for tiger reintroduction in one likely candidate site, the 1100 km² Hupingshan–Houhe National Nature Reserve complex in Hunan and Hubei Provinces, China. Our preliminary analysis estimates that for wild boar, potential summer and winter habitat availability is 372–714 km² and 256–690 km², respectively, whereas for Sika deer, potential summer and winter habitat availability is 443–747 km² and 257–734 km², respectively. Our model identifies potential priority areas for release and restoration of prey between 195 and 790 km² with a carrying capacity of 596–2409 wild boar and 468–1929 Sika deer. Our analysis suggests that Hupingshan–Houhe could support a small population of 2–9 tigers at a density of 1.1–1.2 tigers/100 km² following prey and habitat restorations. Thus, current habitat quality and area would fall short of the target recovery goal. We identify major challenges facing a potential tiger reintroduction project and conclude that restoring the habitat and prey base, addressing concerns of local people, and enhancing coordination across park boundaries are significant challenges to meeting the broader goals of supporting a reintroduced wild tiger population. Tiger range states have committed to doubling the world’s wild tigers by 2022. The results of this study have implications for China’s commitment to this goal and for the future of tiger and other large carnivore reintroduction efforts in Asia and globally.

© 2014 The Authors. Published by Elsevier Ltd. This is an open access article under the CC BY license (http://creativecommons.org/licenses/by/3.0/).

1. Introduction

Human-caused biodiversity loss is a global problem that extends across taxonomic groups and geographic regions (Dirzo et al., 2014). Large carnivores are particularly threatened (Di Marco et al., 2014; Ripple et al., 2014), and the tiger (Panthera tigris) is among the world’s most endangered large carnivores (Tilson and Nyhus, 2010).

The South China tiger (Panthera tigris amoyensis) is a tiger subspecies native to China (Nyhus, 2008) that is considered likely extinct in the wild (Tilson et al., 2004). Numbering more than 4000 as recently as the early 1950s, the South China tiger population in China suffered dramatic declines in the past century due to government eradication, habitat loss, unregulated hunting, and human encroachment into tiger habitat (IUCN, 2011; Tilson et al.,...
2004). It is now the most critically endangered of all tiger subspecies (IUCN, 2011).

The government of China, together with the leaders of tiger range countries, recently declared a goal to double the world’s wild tiger population by 2022 (Global Tiger Summit, 2010; Wikramanayake et al., 2009). Due to the growing awareness of the importance of tiger reintroduction as one strategy to support tiger recovery goals (Driscoll et al., 2012; Tilson et al., 2010), Chinese authorities and international organizations are seeking to identify one or more existing protected areas of sufficient size within the historical range of South China tigers to support wild tiger populations (State Forestry Administration of China, 2010; Tilson et al., 2010). This would be the world’s first large-scale reintroduction of captive tigers back to the wild.

Predator reintroductions can enhance conservation by increasing abundance of the target species and other species that share these habitats (Deinet et al., 2013). Notable recent examples of reintroductions that led to recovery of extirpated populations include wolves in the western United States (Carroll et al., 2006) and Eurasian Lynx in Europe (Deinet et al., 2013). Effective reintroductions can have ecosystem-wide benefits by restoring historic species interactions, including trophic cascades (Ripple et al., 2014).

Since 1994, the Chinese Association of Zoological Gardens (CAZG) has been managing the remaining captive South China tigers (Wang et al., 1995). As of October 2011, there were 108 captive South China tigers descended from the small founding population of six individuals captured between 1958 and 1960 (Wang et al., 1997; Traylor-Holzer et al., 2010). However, these remaining South China tigers face significant challenges to remain viable, including relatively low reproduction rates and low genetic variation (Traylor-Holzer et al., 2010; Yin and Traylor-Holzer, 2011). The organization Save China’s Tigers, with the support of the State Forestry Administration of China (SFA), relocated five of these captive tigers to a private captive facility in South Africa to create a founder stock for possible future reintroduction of tigers back into the wild in China (Tilson et al., 2010). As of October 2011, there were 12 living individuals (four of the original tigers and eight of their offspring) in South Africa (Yin and Traylor-Holzer, 2011).

International tiger experts and the IUCN Cat Specialist Group have proposed a minimum goal for a free-ranging South China tiger population by establishing at least three populations, each consisting of 15–20 tigers living in a minimum of 1000 km² of natural habitat within the historic range of the subspecies (Breitenmoser et al., 2006). Hupingshan–Houhe National Nature Reserve (NNR) complex was identified as the largest and possibly the most suitable location to support a small population of wild tigers (Tilson et al., 2004, 2010). With a total area of 1100 km² the reserve complex is larger than 21 other areas identified as potential high priority tiger landscapes across Asia (Sanderson et al., 2010). The most recent confirmed records of wild South China tigers in this protected area complex were documented over two decades ago (Koehler, 1991), and protected area staff and villagers also reported visual sightings and anecdotal evidence from the 1970s and the 1980s.

Large carnivores like tigers are often difficult to study in forested environments because of their low population densities, large home ranges, and cryptic behavior. This problem is magnified when the target species is extinct in the wild. Consequently, one means of addressing this is to examine prey populations. The literature documents a strong, positive correlation between tiger abundance and prey availability (Karanth et al., 2004; Karanth and Stith, 1999; Karanth and Sunquist, 1995; Sunquist, 2010) and highly correlated activity patterns between tigers and tiger prey (Karanth and Sunquist, 2000; Sunquist, 1981). Therefore, an assessment of habitat suitability of tiger prey may serve as a reasonable proxy to guide tiger restoration efforts, particularly since historic knowledge of tiger habitat use, movement patterns, and diets in this area is limited. Important tiger prey species include forest and grassland ungulates, ranging from small deer such as barking deer (Muntiacus muntjak) (20 kg) and wild boar (Sus scrofa) (30–40 kg) to large animals like water buffalo (Bubalus bubalis) (160–400 kg) and sambar (Cervus unicolor) (185–260 kg) (Karanth et al., 2004; Smith and Xie, 2008; Sunquist, 2010). Tiger predation is non-random; tigers select for medium to large-size prey, and only switch to smaller prey when critical prey species are non-existent or at extremely low densities (Biswas and Sankar, 2002; Karanth and Sunquist, 1995; Sunquist, 2010, 1981).

In this study we used spatial Habitat Suitability Index (HSI) models to demonstrate how estimates of prey distribution and abundance can inform large carnivore restoration. Our specific objectives were to identify: (1) the amount of suitable habitat available for tigers and two prey species in the Hupingshan–Houhe National Nature Reserve complex in China, (2) the approximate prey biomass the two reserves could support, and (3) the sizes and configurations of potential core areas that could support initial release and restoration of both tigers and their prey.

This effort was part of a larger goal to evaluate the feasibility of a South China tiger reintroduction program. As field data for wild South China tiger and prey populations in Hupingshan–Houhe NNR are essentially non-existent, our habitat suitability assessment was developed using Geographic Information Systems (GIS) based on literature reviews, preliminary field work, and expert opinion. Our spatial models provide a preliminary scientific assessment and reference for habitat evaluation, site selection, and conservation planning for a potential South China tiger reintroduction in the Hupingshan–Houhe NNR complex. We conclude with a discussion of key management issues that address potential ecological, landscape, genetic, and institutional challenges facing a tiger reintroduction program. The results of this study have implications for other tiger and large carnivore reintroduction efforts in Asia and globally.

2. Methods

2.1. Study area

The Hupingshan–Houhe National Nature Reserve complex consists of two adjacent NNRS located in south-central China (longitude 110°02' N – 110°59' N, latitude 29°58' E – 30°10' E). Hupingshan NNR is situated along the northern border of Hunan Province adjacent to Houhe NNR in southern Hubei Province (Fig. 1). Covering nearly 1100 km², Hupingshan–Houhe is home to some of China’s most threatened plant and animal species and occurs in the historic range of the South China tiger (Dahmer et al., 2014; Houhe, 2004; Hupingshan, 2004).

Hupingshan–Houhe has an annual average temperature of 9.2 °C, annual average rainfall of 1900 mm, typically experiences hot and wet summers and cold winters, and supports subtropical evergreen and deciduous mixed forests (Houhe, 2004; Hupingshan, 2004). Located in the transition region between the Guizhou Plateau and hilly areas in southeastern China, Hupingshan–Houhe is topographically heterogeneous, including high elevations, deep ravines, and narrow valleys (Houhe, 2004; Hupingshan, 2004; Li et al., 2005; Liu and Pang, 2005; Qin et al., 2006).

The local human population within the protected area complex was estimated to exceed 30,000 in 2002 (27.3 people/km²); however, this estimate is likely unreliable because some residents who emigrated from this area to urban areas are still registered as living in this area (Houhe, 2004; Hupingshan, 2004). The population is characterized by a low annual per capita income.
and a high reliance on farming and livestock husbandry. Limited industry in the area includes coal and phosphate mining. Tourism is a small but growing economic activity. Key biodiversity threats have been identified, including: forest fires, poaching (hunting is not legal), livestock grazing, illegal logging, rapid and unregulated development from urban sprawl, road construction, mines, and factories (Dahmer et al., 2014; Houhe, 2004; Hupingshan, 2004).

### 2.2. Habitat Suitability Index (HSI)

Widely used in ecological assessment and conservation planning, HSI models incorporate expert opinion and/or ecological studies to estimate habitat quality using factors, such as land cover and elevation, considered important for the presence or abundance of a target species (Elith and Burgman, 2003; Klskey et al., 1999; Lopez-Lopez et al., 2007; Luan et al., 2011; Store and Kangas, 2001), especially when species distribution data are lacking (Burgman et al., 2001; Downs et al., 2008; Smith et al., 2007). Variables can be scaled to a single standard to create a relative measure of habitat suitability that is comparable across locations (Brooks, 1997; Elith and Burgman, 2003). Each variable in an HSI is represented using a single suitability index (SI) linked by additive, multiplicative, or logical functions that can best reflect relationships among the variables (Burgman et al., 2001).

Since systematic field studies on ungulates in Hupingshan–Houhe are lacking, we used a comprehensive review of available literature and expert opinion to create HSI models for two tiger prey species. The models identify suitable habitat patches and estimate potential carrying capacity for the two species using variables deemed significant to their habitat requirements as well as proximity to human impacts. Parameters were estimated from research on prey populations in other regions, while adjusting for climate, topography, and vegetation features of Hupingshan–Houhe.

#### 2.2.1. Model prey species selection

Forest and grassland ungulates make up the bulk of a tiger’s diet (Miquelle et al., 1996; Smith and Xie, 2008; Sunquist, 2010). At least nine potential prey species may have lived in Hupingshan–Houhe historically, and camera trap studies (Dahmer et al., 2004; Tilson et al., 2004) and a 2010 line transect survey (Lou et al., 2011) confirmed the presence of at least six prey species (Table 1). In addition to density, ungulate prey size and biomass are often keys to survival and reproduction in wild tiger populations because tigers select for large-size prey with a mean weight around 91.5 kg (Karanth and Stith, 1999; Karanth and Sunquist, 1995, 2000; Miquelle et al., 1996; Sunquist, 1981). Information on the size, conservation status, and estimated current density of possible prey species is summarized in Table 1. Chinese serow (Capricornis milneedwardsii), wild boar (Sus scrofa), and Sika deer (Cervus nippon) are among the relatively large prey species found in Hupingshan (Table 1). Wild boar and Sika deer were selected as model prey species based on expert opinion and lack of field data on Chinese serow (Tilson et al., 2008). Potential suitable habitat for these two species was modeled in GIS to estimate potential prey densities and thus possible tiger abundance.

#### 2.2.2. Prey habitat and area requirements

##### 2.2.2.1. Wild boar

Wild boar are widely distributed across Europe, North Africa, Southeast Asia, Japan, and China, except for dry deserts and high plateaus (Leaper et al., 1999; Smith and Xie, 2008). Wild boar are considered agricultural pests in some areas (Geisser and Reyer, 2004). Habitat use by wild boar is determined in part by food availability, vegetation community, cover from predators, slope, aspect, elevation, distance to water, and weather conditions (Baber and Coblentz, 1986; Leaper et al., 1999).

Wild boar are omnivorous, but plant matter is predominant in their diet, while crops and high energy food are highly preferred (Herrero et al., 2006; Leaper et al., 1999). Wild boar prefer but are not restricted to natural woodlands for shelter and food sources (Leaper et al., 1999; Smith and Xie, 2008). Pinewoods, mixed woodland, scrub, and grasslands provide alternative food resources. These habitat types, however, offer suboptimal shelter (Leaper et al., 1999; Thurfjell et al., 2009). Forest edges and sparsely populated areas are also preferred because they provide more

---

**Fig. 1.** Geographic features of Hupingshan–Houhe National Nature Reserve complex, China.
opportunities for food and shelter (Honda, 2009; Thurfjell et al., 2009).

Wild boar favor lower elevations and gentle slopes, while in warm, dry regions they avoid south slopes where less grass and forbs grow (Baber and Coblentz, 1986; Honda, 2009). In Hupingshan–Houhe, wild boar were found at elevations as high as 1400 m (Dahmer et al., 2004). They select areas with snow depth of less than 40–50 cm because snow hinders their movement (Honda, 2009) and prefer proximity to water for bathing, resting, reproduction, and rearing of young (Baber and Coblentz, 1986; Fernandez-Llario, 2004; Leaper et al., 1999; Thurfjell et al., 2009). Barber and Coblentz (1986) found in California, USA, that wild boar use habitat within 330–370 m to water sources.

The home range of wild boar ranges from 0.7 to 24 km² for females and 1.4–35 km² for males, while density ranges from 2.6 per km² to 15 per km². A summary of different density estimates for wild boar from various relevant study sites is listed in Table 2. Additionally, wild boar has been found to migrate from high (>1000 m) to low (<1000 m) elevation in winter before returning to higher elevations in spring (Igota et al., 2004; Smith and Xie, 2008). In a study in Taohongling Nature Reserve, Jiangxi Province, China, Sika deer showed no selection for aspect, but preferred habitat with slopes between 15° and 45° (Liu, 2007). Additionally, Sika deer prefer habitat where water sources are within 100–400 m (Jiang and Li, 2009).

The home range of Sika deer ranges from 0.2 to 0.6 km² in Boso Peninsula, Japan, while density ranges from the historical record of 3.5–4.5 km² in southern China to 50 km² in Northern Japan (Ito, 2009; Jiang and Li, 2009; Miyashita et al., 2008, 2007; Takada et al., 2002). A summary of density estimates for Sika deer from various study sites is listed in Table 2. Home range, density, and habitat selection of Sika deer are highly correlated with seasonality. In the summer, the Sika deer home range is generally smaller and thus deer are more clustered than during the winter (Maeji et al., 1999; Miyashita et al., 2008).

### 2.2.2.2. Sika deer
Sika deer are widespread across eastern China and also found in southeastern Siberia, Japan, and Korea (Smith and Xie, 2008). Habitat selection by Sika deer also depend on vegetation type, food and water availability, shelter, and snow depth (Honda, 2009; Jiang and Li, 2009).

Sika deer forage in grass, shrub, shrub-meadow, and broad-leaved forests and feed on grass, browse, and occasionally on fruit (Jiang and Li, 2009; Smith and Xie, 2008; Yokoyama, 2009). Sika deer will use agricultural fields adjacent to forest edges but avoid densely populated urban areas (Honda, 2009; Miyashita et al., 2008).

In southern China, Sika deer usually live in mountainous habitat at low elevations (300–800 m), but can range to over 2000 m in western China (Jiang and Li, 2009; Koda et al., 2008; Koga and Ono, 1994). The distribution of Sika deer is also limited by climate, particularly snow depth, as populations tend to descend to lower elevations in winter before returning to higher elevations in spring (Igota et al., 2004; Smith and Xie, 2008). In a study in Taohongling Nature Reserve, Jiangxi Province, China, Sika deer showed no selection for aspect, but preferred habitat with slopes between 15° and 45° (Liu, 2007). Additionally, Sika deer prefer habitat where water sources are within 100–400 m (Jiang and Li, 2009).

### 2.2.3. Model specifications and data preparation
Habitat requirement variables used in our models included: land cover (LC), elevation (ELEV), slope (SLP), distance to water (DW), and distance to forest edge (DFE). Disturbance is represented by distance to areas of potential human impacts (DD), including agriculture, roads, and urban centers. Because these HSI variables are synergistic rather than cumulative, they were linked using a multiplicative function (Brown et al., 2000; Burgman et al., 2001; Williams et al., 2008). In summary, the HSI was a geometric mean of the six habitat variables using the following formula:

\[
HSI = (DD \times LC \times ELEV \times SLP \times DW \times DFE)^{1/6}
\]

Data were obtained from NASA's Shuttle Radar Topography Mission (SRTM), Landsat satellite imagery, GIS data obtained from Chinese authorities, and data we digitized manually (Table 3). ArcGIS 10 (ESRI, Inc.) was used to process and combine thematic

### Table 1
Possible prey species historically present in the Hupingshan–Houhe National Nature Reserve Complex. A survey using line transects estimated current density and total number for some species in the Houhe NNR. VU – vulnerable, EN – endangered, LC – least concern.

| Prey species | Mean weight (kg) | Conservation status | Density (number) in Houhe NNR |
|--------------|-----------------|---------------------|-----------------------------|
| Chinese serow (Capricornis milneedwardsii) | 85–140 | VU | – |
| Chinese water deer (Hydropotes inermis) | 14–17 | VU | – |
| Forest musk deer (Moschus berezovskii) | 6–9 | EN | – |
| Long-tailed goral (Naemorhedus caudatus) | 32–42 | VU | 2.1 ± 0.1 km² (80 ± 4) |
| Reeve’s muntjac (Muntiacus reevesi) | 11–16 | VU | 5.6 ± 0.1 km² (214 ± 6) |
| Siberian roe (Capreolus pygargus) | 20–40 | VU | – |
| Sika deer (Cervus nippon) | 40–150 | EN | – |
| Tuffed deer (Elaphodus cephalophus) | 15–28 | VU | 5.8 ± 0.2 km² (222 ± 6) |
| Wild boar (Sus scrofa) | 50–200 | LC | 7.9 ± 0.3 km² (302 ± 11) |

### Table 2
Wild boar and Sika deer density estimates from selected locations.

| Species | Density (per km²) | Location | References |
|---------|-------------------|----------|------------|
| Wild boar | 2.6 | Pench National Park, India | Biswas and Sankar (2002), Sunquist (2010) |
| | 4.4 | Bardia National Park, Nepal | Sunquist (2010) |
| | 4.4–6.1 | Sumatra, Indonesia | O’Brien et al. (2003) |
| | 7.9 | Houhe NNR, China | Lou et al. (2011) |
| | 15.0 | South Carolina, USA | Saunders and McLeod (1999) |
| Sika deer | 0.5–0.7 | Korea | McCullough (2009) |
| | 3.5–4.5 | Ningguo, China | Jiang and Li (2009) |
| | 8.6 | Lazovsky reserve, Russia | Voloshina and Myasnikov (2009) |
| | 27.6 | Taiwan | Pei (2009) |
| | 50.0 | Kinkazan Island, Japan | Ito (2009), McCullough (2009) |
layers. All layers were projected into Universal Transverse Mercator zone 49 N using the WGS84 datum, and all raster layers were resampled to a cell size of 28.5 × 28.5 m², the native size of the Landsat satellite imagery.

Where the original SRTM elevation data included significant data gaps, we carried out our own interpolation by kriging, using digitized contour lines obtained from China’s State Forestry Administration, and GPS elevation points. We derived slope from the original Digital Elevation Model (DEM) for all intact areas and used the modified SRTM elevation layer for the large interpolated areas. We created a Normalized Difference Vegetation Index (NDVI) using imagery from the Landsat Enhanced Thematic Mapper (ETM+) sensor to assess photosynthetic activity (United States Geological Survey, 2008).

The land cover data layers were obtained from MacDonald Dettwiler and Associates (MDA) federal (MDA Federal, 2008) and are based on a 2000 Landsat ETM + image. Land cover classes located in the study area include deciduous forest, evergreen forest, shrub/grass, grassland, barren/minimal vegetation, urban/built-up, agriculture (general), agriculture (rice/paddy), wetland, and water. However, based on comparison to ground truthing GPS field data points from the Hupingshan–Houhe study area in 2007, some areas originally classified as natural vegetation (e.g., shrub/grass, grassland, and barren/minimal vegetation) are actually agricultural areas. Additionally, this classification scheme failed to identify agricultural areas alongside rivers and roads.

To resolve these overestimations of potential habitat, we used NDVI values to differentiate natural vegetation from agriculture. We gathered ground control points in the field using GPS in 2007 and compared the relative reflectance patterns of known agricultural areas from those with natural vegetation. The mean NDVI value of the agriculture points (0.102 ± 0.013) was significantly different than that of the natural vegetation points (0.423 ± 0.083) (Mann–Whitney U-test, n = 52, p < .001). We then derived a threshold value of 0.275 to divide the shrub/grass, grassland, and barren/minimal vegetation land cover classes into new agricultural or shrub/grassland classes, while keeping the original forest, urban/developed, wetland, water, and agriculture land cover classes intact. We also created 100 m buffers along both sides of all roads and rivers, within which we used the above NDVI thresholds to divide the forest, shrub/grass, grassland, and barren/minimal vegetation classes into either agriculture or shrub/grass classes.

All parameters were constructed on a scale from 0 to 10. Definitions of SI ranges were adapted from other HSI studies and standardized (Brown et al., 2000; Burgman et al., 2001) (Table 4). SI value estimations used in this study linked habitat suitability to population abundance as well as fecundity and survival. A high SI value indicates high relative abundance or density and possibly high fecundities and survivorships (Burgman et al., 2001).

To account for uncertainties in habitat requirement parameterizations in the model, we created three scenarios (high – H, mid – M, and low – L) of suitability indices of habitat requirement for each species (Burgman et al., 2001). We created one scenario for distance to disturbance (DD). Since habitat selection of both species varies seasonally, particularly with elevation change, summer (S) and winter (W) scenarios were also constructed with different elevation parameterizations to accommodate such potential variations. Six HSI scenarios in total were created for each species: three each for summer and winter.

Categorical values were assigned for variables LC, ELEV, and SLP. A summary of suitability indices is presented for wild boar (Table 5) and for Sika deer (Table 6). We used continuous linear functions rather than categorical values to convert DW, DFE, and DD into suitability index values for both species. For DW, we expect that distances closer than 400 m are optimal, with suitability declining at greater distances (Fig. 2). Functions used to convert DFE to SI values were based on species requirements for foraging and shelter as well as daily movement distance. Negative values for DFE represent areas within the forest and positive values represent areas outside the forest. We expect that suitability for prey species would be high to optimal in areas outside the forest and at the forest edge, and would decline steeply just outside the forest (<200 m), at which point suitability would continue to decline gradually (Fig. 3). We assumed a positive correlation between DD and suitability until 1000 m or greater, at which point habitat is optimal (Fig. 4).

Distances were obtained using euclidean distance. Agriculture, grassland/shrub, forest, and urban center land cover classes were extracted from the land cover data. Inside and outside distances to forest edges – borders between forest and shrub/grassland and agriculture – were derived by first generalizing each category from

Table 3
Sources for spatial data used in the habitat suitability analysis for wild boar and Sika deer in Hupingshan–Houhe.

| Model input                  | Source                                                                                                                                 |
|------------------------------|---------------------------------------------------------------------------------------------------------------------------------------|
| Elevation                    | NASA Shuttle Radar Topography Mission (SRTM) Digital Elevation Model Version 3 (2000); elevation contour lines for interpolation from Chinese Academy of Forestry, provided by State Forestry Administration of China (2008) |
| Slope                        | Derived from elevation                                                                                                                                                                               |
| Land cover                   | MDA Federal EarthSat GeoCover LC 2000                                                                                                                                                                |
| Normalized Difference        | Landsat Enhanced Thematic Mapper (2002, 2008)                                                                                                                                                        |
| Vegetation Index (NDVI)      | Land cover classes were extracted from natural vegetation from agriculture, shrub/grass, and barren/minimal vegetation classes. All              |
| Roads                        | Combination of GPS data from Nyhus (2008) and digitized data from maps provided by State Forestry Administration of China (2008)                                                             |
| Water                        | Digitized from maps provided by State Forestry Administration of China (2008)                                                                                                                      |
| Reserve boundaries           | Digitized from Hunan Hupingshan National Nature Reserve Management Plan from the Administration of Hunan Hupingshan National Nature Reserve (2004) |

Table 4
Definitions of suitability index values used in the habitat suitability analysis for wild boar and Sika deer in Hupingshan–Houhe National Nature Reserve complex.

| Suitability index | Description of habitat use                                                                                           |
|-------------------|----------------------------------------------------------------------------------------------------------------------|
| 0–2               | Not suitable: little or no occurrence in field studies; mortality may occur; active avoidance in field studies            |
| 2.01–4            | Least suitable: rare occurrence or very low density in field studies                                                |
| 4.01–6            | Moderately suitable: low occurrence or density in field studies                                                      |
| 6.01–8            | Highly suitable: average occurrence or density in field studies                                                     |
| 8.01–10           | Most suitable: high density or relative abundance in field studies; high growth potential; active preference in field studies |
land cover data and then combining reclassifications of the Euclidean distances. Finally, HSI results were reclassified into five categories, ranging from 0–2 (not suitable) to 8.01–10 (most suitable) in accordance with the SI definitions (Table 4).

### 2.2.4. Potential priority release sites and restoration areas

To identify core areas for possible prey release and restoration in Hupingshan–Houhe we combined HSI values for both wild boar ($HS_{WB}$) and Sika deer ($HS_{SD}$) to estimate total prey suitability ($HS_{Prey}$). Six scenarios of $HS_{Prey}$ were created using corresponding $HS_{WB}$ and $HS_{SD}$ scenarios. To simplify the analysis we assumed complete niche differentiation and no density dependent mortality feedbacks between these two species. Both these assumptions may lead to an overestimation of suitable habitat and potential prey density.

Studies have shown that the relative importance of prey in the tiger diet is correlated with prey biomass density and prey size (Table 7) (Biswas and Sankar, 2002; Miquelle et al., 1996; O'Brien et al., 2002).

### Table 5

| Variable                  | Suitability index | Assumption                                                                 | References                                                                 |
|---------------------------|-------------------|-----------------------------------------------------------------------------|---------------------------------------------------------------------------|
|                           | High              | Medium                       | Low                         |                                                                                      |
| Habitat type              |                   |                               |                             |                                                                                      |
| Forest                    | 10                | 10                           | 10                          | Baber and Coblentz (1986), Leaper et al. (1999), Fernandez et al. (2006), Herrero et al. (2006), Smith and Xie (2008), Honda (2009), Thurfjell et al. (2009) |
| Agriculture               | 8                 | 6                            | 4                           |                                                                                      |
| Shrub/ grassland          | 8                 | 8                            | 6                           |                                                                                      |
| Urban built-up            | 0                 | 0                            | 0                           |                                                                                      |
| Slope (°)                 |                   |                               |                             |                                                                                      |
| 0–15                      | 10                | 10                           | 10                          | Geisser and Reyer (2004), Honda (2009)                                                |
| 15–30                     | 8                 | 8                            | 8                           |                                                                                      |
| 30–45                     | 6                 | 4                            | 2                           |                                                                                      |
| >45                       | 0                 | 0                            | 0                           |                                                                                      |
| Summer elevation (m)      |                   |                               |                             |                                                                                      |
| <1500                     | 10                | 10                           | 10                          | Baber and Coblentz (1986), Leaper et al. (1999), Dahmer et al. (2004), Honda (2009)   |
| 1500–1800                 | 8                 | 6                            | 4                           |                                                                                      |
| >1800                     | 6                 | 4                            | 2                           |                                                                                      |
| Winter elevation (m)      |                   |                               |                             |                                                                                      |
| <1000                     | 10                | 10                           | 10                          |                                                                                      |
| 1000–1800                 | 8                 | 6                            | 4                           |                                                                                      |
| >1800                     | 6                 | 4                            | 2                           |                                                                                      |

### Table 6

| Variable                  | Suitability index | Assumption                                                                 | References                                                                 |
|---------------------------|-------------------|-----------------------------------------------------------------------------|---------------------------------------------------------------------------|
|                           | High              | Medium                       | Low                         |                                                                                      |
| Habitat type              |                   |                               |                             |                                                                                      |
| Forest                    | 10                | 10                           | 10                          | Baber and Coblentz (1986), Maeji et al. (1999), Koda et al. (2008), Miyashita et al. (2008), Smith and Xie (2008), Honda (2009), Jiang and Li (2009), Pei (2009), Yokoyama (2009) |
| Agriculture               | 8                 | 6                            | 4                           |                                                                                      |
| Shrub/ grassland          | 10                | 10                           | 10                          |                                                                                      |
| Urban built-up            | 0                 | 0                            | 0                           |                                                                                      |
| Slope (°)                 |                   |                               |                             |                                                                                      |
| 0–15                      | 10                | 10                           | 10                          | Maeji et al. (1999), Liu (2007), Honda (2009), Jiang and Li (2009)                    |
| 15–30                     | 10                | 10                           | 10                          |                                                                                      |
| 30–45                     | 8                 | 6                            | 4                           |                                                                                      |
| >45                       | 0                 | 0                            | 0                           |                                                                                      |
| Summer elevation (m)      |                   |                               |                             |                                                                                      |
| <1000                     | 10                | 10                           | 10                          | Koga and Ono (1994), Maeji et al. (1999), Igota et al. (2004), Koda et al. (2008), Smith and Xie (2008), Jiang and Li (2009), Takatsuki (2009) |
| 1000–1800                 | 8                 | 6                            | 4                           |                                                                                      |
| >1800                     | 6                 | 4                            | 2                           |                                                                                      |
| Winter elevation (m)      |                   |                               |                             |                                                                                      |
| <800                      | 10                | 10                           | 10                          |                                                                                      |
| 800–1500                  | 8                 | 6                            | 4                           |                                                                                      |
| >1500                     | 6                 | 4                            | 2                           |                                                                                      |
The suitable habitat index for tiger prey selection was calculated using the following formula:

\[ \text{HSI}_{\text{Prey}} = \left( \frac{\text{IS}_{\text{WB}} \times \text{IS}_{\text{SD}}}{D_{\text{FD}}} \right)^{1/2} \]

We identified potential priority areas by selecting habitat patches with HSI values greater than 6 and larger than 1 km² in size. Identified contiguous patches larger than 20 km² as potential priority release sites and smaller patches as priority restoration areas.

2.2.5. Carrying capacity estimation

HSI models typically assume a direct linear relationship with carrying capacity, reflected in population density or biomass per unit area (Rand and Newman, 1998). To estimate the carrying capacity of wild boar and Sika deer in Hupingshan–Houhe, we first extrapolated the number of animals (\( n \)) each square pixel (812.25 m²) can potentially support based on its HSI value. For each pixel (\( i,j \)),

\[ n_{ij} = 0.1 \times \text{HSI} \times d \]

where \( d \) is the average species density estimate (converted to animals per pixel area), \( i \) and \( j \) reference a specific pixel. Because HSI models were constructed based on a 0–10 scale, a coefficient of 0.1 was applied to rescale the HSI to 0–1. Carrying capacity was calculated by summing the density values of each pixel in Hupingshan–Houhe:

\[ K = \sum n_{ij} \]

From the literature (Table 2), we calculated the mean densities for wild boar and Sika deer after excluding the two highest density estimates to reduce the risk of over-estimating potential prey density. We used density estimates (\( d \)) of 4.6 wild boar per km² and 3.6 Sika deer per km². We estimated carrying capacity for both species for the entire Hupingshan–Houhe NNR complex as well as potential priority areas.

3. Results

For each prey species, six different HSI scenarios showed a range of suitable habitats in Hupingshan–Houhe (Figs. 5 and 6). For wild boar, mean HSI values ranged from 5.00 to 5.99 for the summer range, and 4.70 to 5.91 for the winter range (Table 8). Our model identified potential habitat (HSI > 6) for the summer
Table 7
Ungulate species biomass density and relative biomass in tiger diet in India, Russian far east, and Indonesia.

| Prey (mean weight, kg) | Biomass density (kg/km²) | Relative biomass in tiger diet (%) | References |
|------------------------|--------------------------|-----------------------------------|------------|
| **Pench NP, India**    |                          |                                   |            |
| Wild boar (38)         | 98.4                     | 7.7                               | Biswas and Sankar (2002), Sunquist (2010) |
| Sambar (212)           | 1291.1                   | 29.3                              |            |
| Chital (55)            | 4441.3                   | 39.6                              |            |
| Muntjac (20)           | –                        | 2.6                               |            |
| **Sikhote-Alin, Russia** |                        |                                   |            |
| Wild boar (125)        | –                        | 24–29.5                           | Miquelle et al. (1996), Smith and Xie (2008), Takayoshi and Kousaku (2009), Sunquist (2010) |
| Sika deer (45)         | –                        | 0.5                               |            |
| Red deer (180)         | –                        | 63.9                              |            |
| Roe deer (30)          | –                        | 0.9–6.3                           |            |
| **Sumatra, Indonesia** |                          |                                   |            |
| Wild boar (38)         | 190.8                    | –                                 | O'Brien et al. (2003), Smith and Xie (2008), Sunquist (2010) |
| Sambar (212)           | 206.3                    | –                                 |            |
| Muntjac (20)           | 67.7                     | –                                 |            |

* Tiger abundance is found to be significantly correlated with that of the wild boar (p < 0.05) and Sambar (p < 0.1).

![Fig. 5. Summer and winter range Habitat Suitability Index (HSI) models of low to high habitat requirement estimations for wild boar in Hupingshan–Houhe National Nature Reserve complex (HSI: 0–2, not suitable; 2.01–4, least suitable; 4.01–6, moderately suitable; 6.01–8, highly suitable; 8.01–10, most suitable).](image-url)
range with total sizes varying from 372 to 714 km² (35–66% of total area in the reserve complex), while for the winter range, the extent of suitable habitat (HSI > 6) ranged from 256 to 696 km² (24–65% of total area) (Fig. 7A).

For Sika deer, mean HSI values ranged from 5.11 to 6.13 for the summer range, and 4.91 to 6.04 for the winter range (Table 8). Our model identified potential habitat (HSI > 6) for the summer range, where the total areas ranged from 443 to 747 km² (41–69%). Suitable winter range for Sika deer also decreased relative to summer range. The extent of suitable winter habitats (HSI > 6) ranged from 257 to 734 km² (24–68%). The percentages of habitat of different qualities are summarized by the five HSI categories in Fig. 7B.

We identified a range of potential priority areas (HSI > 6, area > 1 km²) (Fig. 8). The extent of total potential priority area
ranged from 195 km² (18%) (LW) to 709 km² (66%) (HS) and the extent of potential priority release sites ranged from 93 km² (9%) (LW) to 610 km² (57%) (HS) (Table 9).

Carrying capacity of prey species in potential priority areas in Hupingshan–Houhe was estimated to range (~25%, +25%) from 596 (447, 745) (LW) to 2409 (1807, 3011) (HS) for wild boar and from 468 (351, 585) (LW) to 1929 (1447, 2411) (HS) for Sika deer (Table 10). For the entire Hupingshan–Houhe area, carrying capacity for wild boar was estimated to range from 2321 (LW) and 2960 (HS) (Fig. 9A). Estimates of carrying capacity for Sika deer ranged from 1895 (LW) to 2370 (HS) (Fig. 9B).

4. Discussion

Our analysis identified potential priority areas, ranging from 195 km² (18%) (LW) to 709 km² (66%) (HS), and current potential priority release sites for wild boar and Sika deer from 93 km² (9%) (LW) to 610 km² (57%) (HS) (Table 9). Although Hupingshan–Houhe is relatively large compared to other protected areas in south-central China (MacKinnon et al., 1996), the limited extent of connected suitable habitat could be a major challenge in meeting the tiger reintroduction goals proposed by international tiger experts and the IUCN Cat Specialist Group.

One of the constraining factors is the complex topography in Hupingshan–Houhe, where about 20% of the NNR is above 1500 m and 38% of the area has a slope steeper than 30°. Additionally, the presence of farmland, towns, and roads in the NNR fragments and limits suitable habitat. To meet the needs of tigers with large home ranges, major habitat restoration and expansion efforts, such as enhancement of corridors among habitat patches and reforestation of degraded area, would be needed in Hupingshan–Houhe.

Tiger territory size is correlated with prey abundance. Increasing prey density is associated with decreasing tiger territory size up to a prey biomass of 2000 kg/km², at which point female territory size levels off (Karanth et al., 2004; Smirnov and Miquelle, 1999; Sunquist, 2010, 1981). In the Russian Far East, tiger population densities are low (0.3–0.7 per 100 km²) due to the relatively short growing season and low primary production to support prey species (Karanth et al., 2004). In comparison, in India and Nepal, tiger population densities can exceed 10 tigers per 100 km² (Karanth et al., 2004; Sunquist, 1981).

Recent field surveys in Hupingshan–Houhe have reported low wild boar abundance (Dahmer et al., 2004; Lou et al., 2011; Tilson et al., 2004). A recent survey of Sika deer found no evidence of this endangered species in the wild in Hunan or Hubei provinces (Jiang and Li, 2009). This deteriorated prey base is a result of illegal harvesting, habitat conversion, and logging (Houhe, 2004; Hupingshan, 2004). Low prey biomass can lead to suppressed tiger reproduction and survivorship, and hence low tiger population densities (Karanth and Stith, 1999). It has been reported that tigers living on a diet mainly consisting of small prey like barking deer (Muntiacus muntjak) may be unable to raise young (Sunquist et al., 1999). The recovery of an assemblage of sufficient large ungulate prey species is thus particularly important for tiger conservation.

In concurrence with field studies in other regions where tiger and prey densities have been studied, one ad hoc method for estimating tiger populations is to assume that an “average tiger” requires 50 ungulate prey animals annually, assuming these are ungulate prey such as deer and wild boar (Karanth and Nichols, 2010). Using an ecological model that predicts that each year tigers crop about 10% of the available prey population, approximately 500 medium-sized prey animals (i.e., wild boar and deer) are needed to support one tiger (Karanth and Nichols, 2010; Karanth et al., 2004). Although the ultimate prey carrying capacity would depend on the nature of the actual species assemblage, considering wild boar and Sika deer as potential critical prey species for reintroduced tigers, our analysis suggest that the potential priority areas could possibly support 2–9 tigers at a density of 1.1–1.2 tigers per 100 km² up to 1.5 tigers per 100 km² assuming a 25% increase in prey abundance. The most optimistic of our carrying capacity estimates for wild boar and Sika deer alone would thus fall short of meeting the minimum goal of supporting 15–20 tigers (Fig. 8). Prey population density could be higher if additional species are available, such as Chinese serow, or if prey species densities were artificially enhanced through supplementation of stock from breeding facilities and with the provision of additional forage (Tilson et al., 2008). As a result, our estimates of potential tiger abundance are likely conservative.

Carrying capacities for wild boar and Sika deer could be constrained by the fragmented habitat, potential interspecific competition, and low quality habitat patches. Another constraint to the prey species is the limited extent of suitable lowland in Hupingshan–Houhe, as demonstrated in our models in which the area of suitable habitat decreased considerably for the winter scenarios for wild boar and Sika deer.

The limited extent of suitable habitat and the current low prey density are likely some of the most daunting challenges, but habi-
tat and prey base restoration in Hupingshan–Houhe would also likely provide extended benefits to the conservation of biodiversity in the area. Hupingshan–Houhe is among the most biologically diverse forest ecosystems in China, home to at least ten globally threatened plant and animal species, and is significant as one of the last large ecosystems within the historic range of the South China tiger (Houhe, 2004; Hupingshan, 2004; Xie et al., 2004).

As a result, even if reintroduced tiger populations remained small, the act of further supporting wildlife protection in these areas, including reducing illegal harvesting of timber and wildlife, could have significant positive impacts on the biological diversity in Hupingshan–Houhe and regional biodiversity conservation goals.

4.1. Model limitations and potential improvements

Uncertainties and errors are inevitable in habitat suitability assessment models. Although HSI models are relatively transparent, some commonly recognized uncertainties and errors in these models include temporal variability, spatial variability, and systematic and random measurement errors (Barry and Elith, 2006; Burgman et al., 2001; Storch, 2002). Our prey models were constructed using information sourced from published literature and expert knowledge. Although suitability index values were defined in the study, there is variability in the information on species habitat preferences. Given the different vegetation types, climates, topographies, and other environmental factors of the various study locations, uncertainties in setting limits and developing functions for suitability index estimations are

![Potential priority areas for prey release and restoration in Hupingshan–Houhe National Nature Reserve complex (HSI: 0–2, not suitable; 2.01–4, least suitable; 4.01–6, moderately suitable; 6.01–8, highly suitable; 8.01–10, most suitable).](image)

**Table 9** Size (km²) of potential priority area for prey release and restoration in Hupingshan–Houhe National Nature Reserve complex under different scenarios.

|          | High | Mid | Low |
|----------|------|-----|-----|
| Release  |      |     |     |
| Summer   | 610  | 493 | 176 |
| Winter   | 591  | 447 | 93  |
| Restoration | 99   | 120 | 139 |
| Total    | 709  | 613 | 315 |

**Fig. 8.** Potential priority areas for prey release and restoration in Hupingshan–Houhe National Nature Reserve complex (HSI: 0–2, not suitable; 2.01–4, least suitable; 4.01–6, moderately suitable; 6.01–8, highly suitable; 8.01–10, most suitable).
inevitable. Limited availability of field data is another constraint. Some data, including snow depth, that may contribute to better predictions of species movement and habitat selection were not available for modeling. Improved data on the number and characteristics of people living within the reserves would also help better model potential human–wildlife conflict for management.

We recognize that HSI models include variables that may be correlated and the strength of the correlation varies (Burgman et al., 2001), but without additional information, we assumed independence of variables used in our model. Errors in remote sensing and GIS technologies are also common. For example, misclassification can cause errors when classifying vegetation cover from satellite data (Shao and Wu, 2008). Finally, our HSI models did not include species population dynamics, i.e., interspecific interactions and density-dependent effects such as social behaviors, which could potentially influence species distribution, movements and ultimately carrying capacity.

To improve the reliability of the model, a study of species distribution and movement is well warranted. Field surveys will help improve and verify variable parameterization, selection, and assignment of relative importance as well as structure of the equation that combines SI values into the HSI model.

### 4.2. Additional considerations and implications

Regardless of the underpinning limitations and uncertainties in the model, suitable areas identified by our HSI models correspond well with the occurrence of prey species from the 2001 camera trap study, except for the records near major roads (Dahmer et al., 2004, 2014). Our study is not intended to provide a fine-grained analysis, but to evaluate the general suitability of the area as the first attempt to analyze the potential for prey and tiger restoration efforts in Hupingshan–Houhe. Our methods have implications for other regions under considerations for tiger recovery efforts where field data are limited.

According to the IUCN/SSC reintroduction guidelines, recovery of prey populations at proposed release site(s) should be addressed before any reintroduction could be considered (IUCN/SSC, 1998). Given that tigers are capable of thriving in environments ranging from the temperate forests of the Russian far east to the jungles of Sumatra, Miquelle et al. (1996) have argued that tigers have few ecological constraints that relate to specific habitat require-

---

### Table 10
Carrying capacity (−25%, +25%) of wild boar and Sika deer in the potential priority area for prey release and restoration in Hupingshan–Houhe National Nature Reserve complex under different scenarios. Density estimates of 4.6 wild boar per km² and 3.6 Sika deer per km² were used.

| Scenario | High | Mid | Low |
|----------|------|-----|-----|
|          | Summer | Winter | Summer | Winter | Summer | Winter |
| Wild boar | Release | 2087 | 2001 | 1615 | 1428 | 616 | 289 |
|          | −25% | 1565 | 1501 | 1211 | 1071 | 462 | 217 |
|          | +25% | 2609 | 2501 | 2019 | 1785 | 770 | 361 |
| Restoration | 322 | 330 | 380 | 355 | 369 | 307 |
|          | −25% | 242 | 248 | 285 | 266 | 277 | 230 |
|          | +25% | 403 | 413 | 475 | 444 | 461 | 384 |
| Total | 2409 | 2331 | 1995 | 1783 | 985 | 596 |
|          | −25% | 1807 | 1748 | 1496 | 1337 | 739 | 447 |
|          | +25% | 3011 | 2914 | 2494 | 2229 | 1231 | 745 |
| Sika deer | Release | 1670 | 1601 | 1270 | 1135 | 478 | 223 |
|          | −25% | 1253 | 1201 | 953 | 851 | 359 | 167 |
|          | +25% | 2088 | 2001 | 1588 | 1419 | 598 | 279 |
| Restoration | 259 | 266 | 302 | 283 | 290 | 245 |
|          | −25% | 194 | 200 | 227 | 212 | 218 | 184 |
|          | +25% | 324 | 333 | 378 | 354 | 363 | 306 |
| Total | 1929 | 1867 | 1572 | 1418 | 768 | 468 |
|          | −25% | 1447 | 1400 | 1179 | 1064 | 576 | 351 |
|          | +25% | 2411 | 2334 | 1965 | 1773 | 960 | 585 |

---

Fig. 9. Carrying capacity estimate of (A) wild boar and (B) Sika deer in Hupingshan–Houhe National Nature Reserve complex based on different Habitat Suitability Index scenarios. Density estimates of 4.6 wild boar per km² and 3.6 Sika deer per km² were used (scenario: high = H, mid = M, low = L, summer = S, and winter = W).
ments except for the direct influence from the abundance and composition of prey species. In addition, tigers have also shown considerable plasticity in predation behavior and relatively quick recovery records given favorable conditions (Sunquist et al., 1999). Restoration of prey species could be enhanced from existing wild boar and deer farms in Hunan and Hubei Provinces ( Tilson et al., 2008 ).

Our HSI analysis and prey carrying capacity model estimates suggest that the size and habitat quality of Hupingshan–Houhe are not ideal compared to high priority tiger conservation landscapes elsewhere in Asia (Sanderson et al., 2006). However, there is adequate habitat that could support a small, highly managed population of tigers if prey species were restored to their full potential and sufficient lowland areas were made available. Land external and adjacent to the two reserves is dominated by people and agriculture, limiting opportunities for reserve expansion or any meaningful corridors to other protected areas. A more nuanced discussion that evaluates additional benefits for both broader biodiversity values and socio-political aspects that might result from the project’s implementation is thus well warranted.

Reintroduction of large carnivores is enormously controversial and carries a high risk of failure when the concerns of local people are not addressed (Breitenmoser et al., 2001; Jiménez, 2009). For any reintroduction of tigers, a comprehensive assessment of the attitudes and needs of local people near possible release sites would be necessary to ensure protection of villagers and their livestock, and a reintroduced population of tigers (IUCN/SSC, 1998). A strategy for meaningful local participation and for mitigating conflicts between local people and reintroduced tigers would need to be established. This is especially critical when reintroducing a species which may prey upon livestock or even people. Given the number of people in the area and limited suitable habitat, creating barriers such as fences would likely be necessary. Additional conflict prevention and mitigation efforts, such as modifying livestock husbandry practices and establishing effective compensation programs, are used in other areas with high potential for tiger-human conflict (Nyhus and Tilson, 2010).

Organizational issues can exert a significant influence on species recovery (Breitenmoser et al., 2001; Jiménez, 2009; Reading et al., 1997). Although Hupingshan and Houhe NNRs are spatially contiguous, they adjoin along the Hunan–Hubei provincial boundary and have separate, independent management structures: each reserve has its own park office, directors, staff, and management plan. Coordination among authorities across park and provincial boundaries is imperative to develop coherent management goals and objectives for habitat restoration and expansion, prey base recovery, management of human–wildlife conflict, and ultimately the survival of free-ranging tiger populations.

Finally, the population of captive South China tigers available for reintroduction is small and genetic diversity is a concern (Traylor-Holzer et al., 2010). At a minimum, intensive genetic and meta-population management in collaboration with the Chinese Association of Zoological Gardens would be needed, and hybridization with other tiger subspecies might need to be considered for long-term viability (Qin, 2012).

5. Conclusions

The global tiger conservation community and tiger range states have committed to doubling the world’s wild tiger population by 2022. Reintroduction of captive tigers into the wild may be one important step towards achieving this goal. The Government of China and international researchers have identified Hupingshan and Houhe National Nature Reserves as one potential release site.

Our analysis of potential prey and tiger suitability within the 1100 km² Hupingshan–Houhe NNR complex suggests that the habitat currently available is fragmented and dominated by upland forests, steep slopes, agricultural lands, and substantial human populations. At best, this area currently would support only a small population of 2–9 tigers and would require intensive management to sustain tigers and prey and to mitigate human–wildlife conflict. A larger tiger population would likely be possible only if more area and in particular more lowland habitat—now largely dominated by people and agriculture—was available to support a more robust prey base. At present, it is likely that too many people live within the reserve complex to justify a free-ranging population of tigers.

At the same time, the area likely represents the largest remaining protected area complex within the historic range of South China tigers, and tigers were recorded in the area within the past four decades. Our analysis identifies potential priority restoration areas that would support modest tiger reintroduction and recovery goals, assuming appropriate attention to the needs and safety of local communities as per IUCN reintroduction guidelines (IUCN/SSC, 1998). Conservation and restoration of former tiger habitat would meet other biodiversity conservation objectives associated with the high biodiversity value currently represented within these reserves (Muntifering et al., 2010) and could help catalyze conservation education and awareness programs and scientific research that further supports national and global biodiversity conservation objectives.

If free-ranging tigers are ever to return to south-central China, long-range planning is needed to identify areas that can in the future become sufficiently large, connected, and protected to maintain an adequate prey base and to address the needs of local people to sustain a viable population of large carnivores. Large landscape conservation efforts in Europe and North America have shown this is possible over time, and China could become a conservation leader in developing this vision in Asia.

Acknowledgements

This research was made possible with support of and through a Memorandum of Understanding between the South China Tiger Advisory Office and the National Wildlife Research and Development Center, National Academy of Forestry, State Forestry Administration (SFA) of the People’s Republic of China. Numerous individuals and organizations supported earlier discussions or field work, including: Wang Wei, Director of Forestry, SFA; Wang Weisheng, Director, and Ruan Xiangdong, Deputy Director, Wildlife Management Divisions, SFA; SFA staff and collaborators in Hubei and Hunan Provinces, including Gui Xiaojie, Director of the Nature Conservation Division, Forestry Department of Hunan Province; Wang Guoping, Director, Hunan Forestry Department; the park directors at Hupingshan and Houhe National Nature Reserves and their staff, particularly Tian Shurong; and other collaborators including Hu Defu and Wang Bin. We thank Tara Harris, Department of Conservation, Minnesota Zoo, and Kevin Potts for their ideas and input. We appreciate the financial and logistical support of the Minnesota Zoo Foundation, Colby College, Andrew W. Mellon Foundation, the Gary and JoAnn Fink Foundation, Columbus Zoo, Woodland Park Zoo, Ecosystems Ltd., Round River Conservation Studies, International Business and Cooperation Agency of the Netherlands, and Gisbert Nollen of International Consultancy Europe. We appreciate support for digitizing and other GIS work by: Rob Mehlich, Jr., Brendan Carrol, Carolyn Hunt, Caitlin Dufraine, Greg LaShoto, Katie Renwick, and Noah Teachey. We are particularly indebted to co-author and South China Tiger Advisory Office Founder and Director Dr. Ronald Tilson, who passed away unexpectedly before this study was published.
References

Agetsuma, N., Sugira, H., Hill, D.A., Agetsuma-Yangahira, Y., Tanaka, T., 2003. Population density and group composition of Japanese sika deer (Cervus nippon yesoensis) in an even-aged broad-leafed forest in Yokushima, southern Japan. Ecol. Res. 18, 475–483.

Andrezjewski, R., Zejerski, W., 1978. Management of a wild boar population and its effects on commercial land. Acta Theriol. 23, 309–339.

Baber, D.W., Coblenz, B.E., 1986. Density, home range, habitat use, and reproduction in feral pigs on Santa Catalina Island. J. Mammal. 67, 512–525.

Barry, S., Elith, J., 2006. Error and uncertainty in habitat models. J. Appl. Ecol. 43, 418–423.

Biswas, D., Sankar, K., 2002. Prey abundance and food habit of tigers (Panthera tigris tigris) in Pench National Park, Madhya Pradesh, India. J. Zool. 256, 411–420.

Borkowski, J., Furubayashi, K., 1998. Home range size and habitat use in radio-collared female sika deer at high altitudes in the Tanzawa Mountains, Japan. Ann. Zool. Soc. 35, 181–186.

Breitenmoser, U., Breitenmoser-Würsten, C., Carbyn, L.N., Funk, S.M., 2000. Assessment of carnivore reintroductions. In: Cittadini, J.L., Funk, S.M., Macdonald, D.W., Wayne, R.K. (Eds.), Carnivore Conservation. Cambridge University Press, Cambridge, UK, pp. 241–281.

Breitenmoser, U., Tilson, R., Nyhus, P., 2006. Reintroduction of the Chinese tiger. Cat News 44, 15.

Brooks, R.P., 1997. Improving habitat suitability index models. Wildl. Soc. Bull. 25, 163–167.

Brown, S., Buja, K., Jury, S., Monaco, M., Banner, A., Baber, D.W., Coblentz, B.E., 1986. Density, home range, habitat use, and reproduction in feral pigs on Santa Catalina Island. J. Mammal. 67, 512–525.

Carroll, C., Phillips, M., Lopez-Gonzalez, C.A., Schumaker, N.H., 2006. Defining recovery goals and strategies for endangered species: the wolf as a case study. Bioscience 56, 25–37.

Dahmer, T.D., Xiaoje, G., Shurong, T., 2004. Camera-trapping to determine the status of South China Tiger in Hupingshan national nature reserve, Hunan province. In: The XXIX International Congress of Zoology. China Zoological Society, Beijing, China.

Dahmer, T.D., Xiaoje, G., Shurong, T., 2014. Camera-trapping to determine the status of South China Tiger in Hupingshan National Nature Reserve, Hunan Province. Chinese J. Wildl. 35, 19–25.

Deinet, S., Ieronymidou, C., McRae, L., Burfield, I.J., Foppen, R.P., Collen, B., Böhm, M., 2013. Wildlife Comeback in Europe: the recovery of selected mammal and bird species. Final report to Rewilding Europe by ZSL. BirdLife International and the European Bird Census Council. ZSL, London, UK.

Di Marco, M., Breitenmoser, U., Breitenmoser-Würsten, C., Carbyn, L.N., Funk, S.M., 2000. Behavioural correlates of predation by tiger (Panthera tigris), leopard (Panthera pardus) and dhole (Cuon alpinus) in Nagarabode, India. J. Zool. 250, 255–265.

Dahmer, T.D., Xiaojie, G., Shurong, T., 2004. Camera-trapping to determine the status of South China Tiger in Hupingshan national nature reserve, Hunan province. In: The XXIX International Congress of Zoology. China Zoological Society, Beijing, China.

Driscoll, C.A., Chestin, I., Jungius, H.O.P., Darman, Y.A., Dinerstein, E., Seidensticker, J., Brown, S., Buja, K., Jury, S., Monaco, M., Banner, A., Baber, D.W., Coblentz, B.E., 1986. Density, home range, habitat use, and reproduction in feral pigs on Santa Catalina Island. J. Mammal. 67, 512–525.

Dahmer, T.D., Xiaoje, G., Shurong, T., 2014. Camera-trapping to determine the status of South China Tiger in Hupingshan National Nature Reserve, Hunan Province. Chinese J. Wildl. 35, 19–25.

Deinet, S., Ieronymidou, C., McRae, L., Burfield, I.J., Foppen, R.P., Collen, B., Böhm, M., 2013. Wildlife Comeback in Europe: the recovery of selected mammal and bird species. Final report to Rewilding Europe by ZSL. BirdLife International and the European Bird Census Council. ZSL, London, UK.

Dahmer, T.D., Xiaoje, G., Shurong, T., 2014. Camera-trapping to determine the status of South China Tiger in Hupingshan National Nature Reserve, Hunan Province. Chinese J. Wildl. 35, 19–25.
