**RESEARCH ARTICLE** 



# Amur tigers and leopards returning to China: direct evidence and a landscape conservation plan

Tianming Wang · Limin Feng · Pu Mou · Jianguo Wu · James L. D. Smith · Wenhong Xiao · Haitao Yang · Hailong Dou · Xiaodan Zhao · Yanchao Cheng · Bo Zhou · Hongyan Wu · Li Zhang · Yu Tian · Qingxi Guo · Xiaojun Kou · Xuemei Han · Dale G. Miquelle · Chadwick D. Oliver · Rumei Xu · Jianping Ge

Received: 23 June 2015/Accepted: 12 September 2015/Published online: 25 September 2015 © Springer Science+Business Media Dordrecht 2015

#### Abstract

*Context* The Amur tiger and leopard, once roaming over the Eurasian continent, are now endangered and confined to the Sikhote-Alin Mountains, Russia—a landscape that has been increasingly fragmented due to human activities. The ultimate fate of these big cats depends on whether they can resettle in their previous main historical range in NE China. Recent sightings of these animals along the China–Russia border have aroused new hope, but direct evidence is lacking.

Tianming Wang and Limin Feng contributed equally to this work.

T. Wang  $\cdot$  L. Feng  $\cdot$  P. Mou  $\cdot$  W. Xiao  $\cdot$ 

H. Yang  $\cdot$  H. Dou  $\cdot$  X. Zhao  $\cdot$  Y. Cheng  $\cdot$ 

B. Zhou  $\cdot$  H. Wu  $\cdot$  L. Zhang  $\cdot$  X. Kou  $\cdot$ 

R. Xu  $\cdot$  J. Ge ( $\boxtimes$ )

State Key Laboratory of Earth Surface Processes and Resource Ecology, Ministry of Education Key Laboratory for Biodiversity Science and Engineering & College of Life Sciences, Beijing Normal University, Beijing 100875, China e-mail: gejp@bnu.edu.cn

#### J. Wu

School of Life Sciences & School of Sustainability, Arizona State University, Tempe, AZ 85287, USA

#### J. Wu

Center for Human-Environment System Sustainability, State Key Laboratory of Earth Surface Processes and Resource Ecology, Beijing Normal University, Beijing 100875, China *Objectives* The main objectives of our study were (1) to determine the abundance and spatiotemporal patterns of tigers, leopards, and primary prey; (2) to investigate factors influencing the resettlement of the two big cats; and (3) to propose a landscape-scale conservation plan to secure the long-term sustainability of the Amur tiger and leopard.

*Methods* We monitored the two felids, their prey, and human activities, with 380 camera-trap stations, for a total of 175,127 trap days and over an area of  $6000 \text{ km}^2$  in NE China. We used the constraint line method to characterize cattle grazing and human influences on tigers, leopards, and their prey species.

#### J. L. D. Smith

Department of Fisheries, Wildlife and Conservation Biology, University of Minnesota, Saint Paul, MN 55108, USA

#### Y. Tian

State Key Laboratory of Environmental Criteria and Risk Assessment, Chinese Research Academy of Environmental Science, Beijing 100012, China

#### Q. Guo

College of Forestry, Northeast Forestry University, Harbin 150040, China

X. Han NatureServe, Arlington, VA 22203, USA

#### D. G. Miquelle Wildlife Conservation Society, Russian Program, Bronx, NY 10460, USA

*Results* Our results show that, unexpectedly, at least 26 tigers and 42 leopards are present within China, which are confined primarily to a narrow area along the border with Russia. We have further identified that cattle grazing and human disturbances are the key hurdles to the dispersal of the tigers and leopards farther into China where suitable habitat is potentially available.

*Conclusions* Amur tigers and leopards are returning to China, indeed, but their long-term resettlement is not likely without active and timely conservation efforts on landscape and regional scales. To overcome the hurdles to the resettlement of tigers and leopards in China, we propose a "Tiger and Leopard Resettlement Program" that will engage the government, local communities, and researchers, so that the long-term sustainability of the Amur tigers and leopards can be ensured.

**Keywords** Panthera tigris altaica · Panthera pardus orientalis · Camera-trapping · Human disturbance · Cattle control · Nature reserve · Conservation planning

## Introduction

The endangered Amur (or Siberian) tiger (Panthera *tigris altaica*) and the critically endangered Amur leopard (Panthera pardus orientalis) both were at the brink of extinction in the late 1990s in Northeast China (Jutzeler et al. 2010; Miquelle et al. 2010a; Feng et al. 2011), which was the central part of their historical distribution range before World War II (Tian et al. 2009; Miquelle et al. 2010b). Due mainly to habitat loss, landscape fragmentation, prey depletion, and poaching, the tiger population declined from more than 3000 to about 500 during the past century (Tian et al. 2009; Miquelle et al. 2010b; Tian et al. 2011; Tian et al. 2014), while the leopard population reportedly had only about 30 individuals (Pikunov et al. 2009; Hebblewhite et al. 2011). Once roaming over a region of 1.85 million km<sup>2</sup>, the Amur tiger is now confined to two separate areas: the Sikhote-Alin

School of Forestry and Environmental Studies, Yale University, New Haven, CT 06511, USA

Mountains of Russia, with a population of 415-490 individuals (Miquelle et al. 2006; Tian et al. 2009), and the southwest Primorskii Krai of Russia-Hunchun of China region, with fewer than 20 individuals (Pikunov et al. 2003; Miquelle et al. 2006; Henry et al. 2009; Sugimoto et al. 2012). The Sikhote-Alin and Southwest Primorskii Krai habitat patches have long been separated by urban development and wetlands (Hebblewhite et al. 2011, 2014), resulting in genetic divergence between the two tiger populations (Henry et al. 2009). The northern habitat is connected with the Wandashan Mountains in China, where tigers are regularly reported (Jiang et al. 2014), but due to the lack of ecological corridors caused by extensive agricultural development, the latter are cut off from other potentially suitable habitat in China. The southern habitat is also home to the only population of the Amur leopard (Pikunov et al. 2009; Hebblewhite et al. 2011), and provides the primary source populations for the possible recovery of the two felids in Northeast China. However, the small and isolated populations of tigers and leopards are at the risk of extinction from genetic, demographic, and environmental stochasticities (Uphyrkina et al. 2002; Henry et al. 2009; Sugimoto et al. 2014). Tiger populations of such small size, especially after being isolated for 20-30 years, could drop to a threshold level below which recovery is impossible unless habitat is increased substantially within one to two generations (Kenney et al. 2014). The only additional potential habitat for these two felids now resides in China (Hebblewhite et al. 2012).

During the past two decades, the endangered status of the two felids has prompted increasing research interests and conservation efforts in China (Zhou et al. 2008; Tian et al. 2009, 2011; Hebblewhite et al. 2012). China's new environmental policies, especially "The Natural Forests Protection Program" initiated in 1998, have led to substantial improvements in the quantity and quality of forests in Northeast China (Wei et al. 2014), which is concurrent with a major tiger conservation effort on the Russian side. Meanwhile, reports of sighting tigers and leopards on the Chinese side have increased in recent years (Zhou et al. 2008; Feng et al. 2011; Jiang et al. 2014; Soh et al. 2014; Wang et al. 2014). Is this really a sign of the tigers and leopards returning to China? Are they "tourists" or "residents" at the crossroads? How can the long-term viability of tigers and leopards be ensured through conservation

C. D. Oliver

planning? Here we address these questions by analyzing the movement trajectories, reproductive behavior, and habitat conditions of the tigers and leopards based on an unprecedented camera-network data.

## Methods

## Study area

Our study area is located in the northern portion of the Changbai Mountain in Jilin and Heilongjiang Provinces in Northeast China, bordering Southwest Primorye, Russia to the east and North Korea to the south west (Fig. 1a). This region is considered the highest priority Tiger Conservation Area in China because it has the largest network of habitat patches which is connected with tiger and leopard source populations in Russia (Hebblewhite et al. 2012). It is a mountainous landscape and has a rugged terrain with elevation varying from 5 to 1477 m. The major vegetation types include Korean pine Pinus koraiensis forests, deciduous birch and oak forests, coniferous forests, natural shrublands, and agricultural areas (Tian et al. 2011; Hebblewhite et al. 2012). The majority of forests have been logged, and many lowelevation forests have been converted to secondary deciduous forests during the past decades (Li et al. 2009). Ungulate species that are potential tiger and leopard prey include the Siberian roe deer (Capreolus pygarus), the sika deer (Cervus nippon) and wild boar (Sus scrofa) (Tian et al. 2011; Xiao et al. 2014). Other predators, including the Asiatic black bear (Ursus thibetanus), Eurasian lynx (Lynx lynx) and the sable (Martes zibellina), coexist with the two big felids in our study area.



Fig. 1 Map of the long-term camera-trap survey network in NE China, with the *insets* showing two wild Amur tiger and leopard individuals photographed in China in 2007 and 2010, respectively. The area enclosed by *blue lines* (*solid* and *dashed*) is the geographic extent of the proposed Tiger and Leopard Resettlement Program (Phase I and II). *Red dashed lines* indicate potential routes for the two felids to migrate back to the Lesser Xing'an Mountains and the Changbai Mountains from Russia. The camera-trap network consists of several areas: site 1 indicates the location of the  $6000 \text{ km}^2$  area of which data are analyzed in this study (see "Methods"), site 2 was set up in 2013, sites 3 and 4 were implemented in 2010, sites 5–7 were installed in 2014. TS is a camera-trap survey transect that became operational in 2007

## Study design and field methods

We established the first long-term camera-trap survey network in Northeast China beginning in 2007, according to potential habitat and historical information on the movement patterns of the two felids (Fig. 1). The camera-trap network was further expanded to cover seven study sites and a transect by 2014. During our study period, tigers and leopards did not appear in all the surveyed areas, but were only found in the Hunchun Nature Reserve and surrounding areas (site 1 in Fig. 1). Thus, our analysis here is based on 2 years (2012-2014) of continuous observations from site 1, which covers an area of 6000 km<sup>2</sup> that includes Laoyeling reserve, Hunchun reserve, Wangqing reserve and Hunchun Forest Bureau land (Fig. 2a). The study area was gridded to  $3.6 \times 3.6$  km cells each of which, except for those in farmland, villages and water, had at least one camera-trap station (380 in total). Cameras were placed usually in pairs along trails, roads and ridges that are natural routes for tigers, leopards and prey. Traps were operated continuously throughout the year. Each camera was visited monthly to download photos and check batteries. The data from 320 stations were used for analysis from August, 2012 to July, 2014 another 60 stations in the southwest of the study area started from May, 2013 to July, 2014. Livestock depredation data from 2008 to 2014 were provided by the Wildlife Depredation Compensation Office, Forestry Department, Jilin Province. Geophysical and human infrastructure data were obtained from China fundamental geographic information dataset, and all data were analyzed using ArcGIS.

#### Data analyses

We analyzed tigers, leopards, their major wild prey (sika deer, wild boar and roe deer), domestic livestock, and human disturbances (e.g., fungus collection, frog breeding, and border patrol) as "entities" from camera traps. We identified each tiger or leopard by its unique pelage pattern; determined sex and classified animals as adult, subadult, or cub based on photographic and video evidence. Specifically, the identification of felid individuals was carefully done through two processes. First, we used the Extract Compare software (http://conservationresearch.org.uk/Home/ExtractCom pare/index.html) to identify individual animals from their natural markings based on the photos from our field cameras. Second, all identified individual animals were then independently verified by two trained experts in Thailand, both confirmed the identity of each and every tiger and leopard individual.

Adult tigers were considered residents if they were photographed in the same area for at least two consecutive years, or observed with cubs (Smith et al. 1987; Barlow et al. 2009; Simcharoen et al. 2014). We calculated a relative abundance index (RAI) (O'Brien et al. 2003) from August, 2012 to July, 2014 for each entity at each trap station as the number of detections per 100 camera-trap days. To avoid inflated counts caused by repeated detections of the same event, only one record of a species/0.5 h was included in the data analysis. To map out the spatial patterns of each entity, the values of RAI for each entity at each station were interpolated using the ordinary Kriging method in ArcGIS 10.0 (ESRI Inc., Redlands, CA, USA). The prediction error measurements generated by Kriging models were used for model selection, and the overall power of the interpolation model was computed.

Relationship between animals and human disturbance appear as point clouds with informative edges, which cannot be approached by traditional regression methods. Constraint lines-the boundaries that delimit point clouds in bivariate scattergramshave been applied in macro-ecology to describe and quantify the effects of limiting factors on response variables (Thomson et al. 1996; Guo et al. 1998; Horning 2012). We applied the constraint line method to characterize cattle grazing and human limits on wildlife species. Data used for this analysis are normalized RAI.

We use R package "overlap" to estimate the overlapping of the activity patterns of tigers, leopards and human presence along the border with Russia (Ridout and Linkie 2009). Land use and land cover maps were created using the unsupervised classification method for 2009 MODIS NDVI satellite imagery (Tian et al. 2011). Thirty cover types were generated first and then merged into six types. The classification accuracy was verified using Google Earth Maps and 1070 ground-based points from field trips. The Kappa coefficient of land cover classification was 0.84.



**Fig. 2** Spatial patterns of the relative abundance index (RAI) for animal species and human activities in the camera-trapping study area, NE China: **a** the grid of camera-trap stations for site 1 in Fig. 1; **b** Amur tiger, **c** Amur leopard, **d** sika deer, **e** wild boar,

**f** roe deer, **g** cattle grazing, **h** human disturbances; and **i** cattle depredation events between 2008 and 2014. All the maps of RAI were generated through ordinary Kriging

# Results

## Tigers and leopards returning to China

From August 2012 to July 2014, we obtained 42,377 independent entity records from 380 camera trap stations, which operated for a total of 175,127 trap days. We photographed 26 tiger individuals, including 15 adults (>2 years old; seven males, six females, and two of unknown sex), five subadults (1–2 years old; two males, two females, and one of unknown sex), and six cubs (<1 year old) born during the study period. The spatial pattern of the relative abundance index (RAI, the number of photographs of the target species per 100 trap days) reveals that tigers were concentrated along the China-Russia border, with 22 of the 26 animals (85 %) spotted within <5 km to the border (Fig. 2b).

Five female adult tigers resided around the border with little territorial overlap for two consecutive years, suggesting they are resident, breeding individuals. One female (TIG-05) was first photographed in August 2012, with three subadults (two females and one male) wandering along the border (T1 area in Fig. 3), and photographed again about 20 km from the border in November 2013, with four young cubs (about 3 months old). She subsequently moved farther westward into China as all her later occurrences were spotted between 10 and 50 km from the border (T2 in Fig. 3). Her previous territory near the border was taken over by her 3-year-old daughter (TIG-05-03) (T3 in Fig. 3). This increased the number of resident female tigers in China to six in 2014. At least two of the adult-sized male tigers also appeared to have breeding territories. One of them (TIG-02) was camera trapped while wandering in an area that encompassed all five border females in 2013. But his movement during 2014 was restricted only to the southern part of that area (including four females), while the northern part was occupied by a male (TIG-08). Our photo records indicate that these two males had little overlap in their movement range.

We also photographed 42 leopards, including 40 adults (>1.5 years old; 21 males, 17 females, and two of unknown sex) and two cubs (<1 year old). The RAI map of leopards indicates that they were also concentrated along the border (Fig. 2c). Thirty-six of the 42

Fig. 3 Illustration of the patterns of migration and settlement of tigers and leopards in China. T1 and T2 were the territories of TIG-05 who gave birth in 2011 and 2013, respectively. T3 and T4 were territories of TIG-05-02 (female) and TIG-05-01 (male). respectively, both were offspring of TIG-05 in 2011. L1 and L2 were the territories of two leopard families. The No. 4 female leopard of family L2 gave birth to 2 cubs (1 female and 1 unknown sex) in June, 2013; both cubs were currently alive and healthy in inland China. F female, M male, and numbers denote time periods of sighting



leopards were located within 5 km from the border. The leopards have had even greater reproductive success within China than tigers. Two leopard families have established their territories 50 km away from the border (L1, L2 of Fig. 3). One female (L2), with two cubs (<5 months old), was videotaped in October 2013 and has lived in this area for more than 2 years.

## Major hurdles for resettlement in China

Our data provide the most direct and comprehensive evidence so far that the Amur tigers and leopards are returning to China in large numbers. But why have they not penetrated farther into China? What are the major hurdles to their resettlement in China? We address these questions by looking into the distribution and abundance of major prey species and human activities. Our analysis indicates that three major factors are responsible for the observed patterns of the returning tigers and leopards. First, a road-cultivation zone-consisting of road, farmland, and villages and running parallel to the border (Fig. 3)—cut across the region and altered animal movement patterns. Apparently, this zone did not completely block tigers and leopards from crossing it because more than 370 cattle depredations occurred on both sides between 2008 and 2014 (Fig. 2i).

Second, two primary prey species of tigers and leopards are either absent (red deer, *Cervus elaphus*), or restricted largely to a zone within about 5 km from the border (sika deer) (Fig. 2d). While wild boars and roe deer are relatively abundant across the entire region (Fig. 2e, f), the distribution pattern of sika deer



**Fig. 4** Relative abundance (RAI) index of tiger versus sika deer, showing a strong positive correlation

closely matches that of tigers and leopards, as evidenced by the positive correlation between sika deer and tigers in terms of the RAI ( $R^2 = 0.58$ , P < 0.05) (Fig. 4). Previous studies also reported that the presence of viable populations of large deer and wild boar were essential for the persistence of tigers (Miquelle et al. 2010b; Hayward et al. 2012).

The third and more severe hurdle, suggested by the similar spatial patterns of sika deer and the felids, is cattle grazing, together with human disturbances such as fungus collection, frog breeding, ginseng farms, and border patrol. In general, the spatial patterns of cattle grazing and human disturbances (Fig. 2g, h) were negatively correlated with those of tigers, leopards, and sika deer (Fig. 2b–d). Our constraint lines analysis (see "Methods") further confirms that cattle grazing and human disturbances played a key role in shaping the distribution of tigers, leopards, and sika deer (Fig. 5).

Browsing cattle triggered about 35 % of the field camera stations and accounted for more than 10 % of all photo events (Fig. 6). The average stocking rate in the Hunchun area was 8 cattle/km<sup>2</sup> between 1989 and 2012 (Fig. 7), and cattle were left unattended, roaming freely from spring to fall (Fig. 8). This high-intensity and free-ranging cattle grazing posed a major disturbance to tigers and leopards, severely confining their movement patterns and distribution limits (Fig. 5a, b) and eventually affects their viability (Ahearn et al. 2001). Importantly, the larger-sized cattle have a strong competitive edge over the sika deer (Fig. 5c).

Human occurrences were detected by 89 % of the field camera stations and accounted for 64 % of all photographed events (Fig. 6), indicating that human influences were broader in space and higher in frequency than cattle, particularly in the northern part of the study area where the cattle grazing was absent (Fig. 2h). But their constraining effects on the felids were much weaker than cattle grazing (Fig. 5d–f). The scattering points above the constraint lines correspond mainly to people patrolling along the border during daytime when the felids are less active (Fig. 9).

## Discussion

Problems of being small and overcrowded

China's long-term conservation objective for the Amur tiger and leopard is to reestablish viable Fig. 5 Constrained patterns of tigers, leopards, and sika deer with respect to cattle grazing and human disturbances. RAI values of tigers (a, d), leopards (b, e), and sika deer  $(\mathbf{c}, \mathbf{f})$  are plotted as a function of cattle grazing intensity and human disturbances separately, using the constraint lines method. The abundance of tigers, leopards, and sika deer decreases with the increasing intensity of cattle grazing and human disturbances, implying a limit on the distribution of these animals. Scattering points enclosed in the dashed circle correspond mainly to people walking along border roads, which were not used in constraint line analysis



populations in a healthy regional ecosystem. As we have shown, the existing populations of these two species in the Hunchun-Primorskii Krai region are too small to be viable at present. Specifically, only 10–14 breeding females are estimated in this tiger population (Pikunov et al. 2003; Sugimoto et al. 2012). Based on our camera trap data and those in the Leopard Land National Park, Russia (LLNP) (http://leopard-land.ru/), the total population of leopards is not less than 80, with about 25–30 breeding females. These cat populations, albeit small, have already far exceeded the carrying capacity of this region (about 4000 km<sup>2</sup> suitable habitat) as per their home-range requirements (Goodrich et al. 2010).

Thus, their reproductive and survival rates are expected to decline (Carroll and Miquelle 2006; Tian et al. 2011). Furthermore, the confined distribution of the tiger and leopard populations makes them vulnerable to genetic, demographic, and environmental stochasticities as well as infectious diseases such as the canine distemper virus outbreak that has been documented for tigers in parts of Sikhote-Alin (Gilbert et al. 2014).

In addition, our results have showed that competition between livestock and large prey is a major constraint to the population growth of Amur tigers and leopards. Especially, cattle grazing limits the spatial distribution of sika deer who are the dominant ungulate in the diet of the two felids (Miquelle et al. 1996; Hebblewhite et al. 2011; Kerley et al. 2015). Our findings are in contrast with previous studies in Lao PDR and Nepal where the tiger abundance is reduced by increased human–tiger conflicts (Johnson et al. 2006; Gurung et al. 2008). However, studies elsewhere also reported that cattle displaced mule deer *Odocoileus hemionus* and zebra *Equus burchelli* in North America and Africa (Stewart et al. 2002; Young et al. 2005) and wild deer *Axis axis, Cervus unicolor*,



Fig. 6 Relative abundance index (RAI) (top) and percentages (bottom) of tiger, leopard, prey species, and human disturbance in the camera trap monitored area

and *Bos gaurus* in India (Madhusudan 2004; Dave and Jhala 2011).

#### A proposed tiger and leopard resettlement program

To ensure the long-term viability of tiger and leopard populations in China and Russia, a cross-border conservation region encompassing existing populations and much more potential habitat must be established in the next several years. This is quite urgent because 42 % of the observed tigers in our database are cubs and subadults whose persistence requires much larger habitat. Based on habitat suitability modeling, Hebblewhite et al. (2012) identified potential habitat for tigers in China, and proposed several "top conservation areas", without considering human disturbances, source populations, and landscape resistance to animal dispersal. Here we propose a comprehensive 3-phase "Tiger and Leopard Resettlement Program (TLRP)" within China (Fig. 1), which can help restoring the populations of the two felids and promoting sustainable livelihoods of the local people.

Phase I is to incorporate a core forest area—the Hunchun Forest Bureau land—into the existing reserve network that currently consists of three nature reserves (Hunchun, Wangqing, and Laoyeling) (Fig. 2a). This will increase the total reserve area



Fig. 7 The number of cattle in Hunchun, China during 1989–2012 (Jilin Statistical Bureau 2013)



Fig. 8 Seasonal relative abundance index (*top*) and activity patterns (*bottom*) of cattle for August 2012–July 2014 in the monitored area



**Fig. 9** Temporal overlap of daily activity patterns among tigers, leopards, and humans along the China–Russia border. The estimated coefficient of overlap,  $\hat{\Delta}$ , has values between 0 [no overlap] and 1 [complete overlap], represented by the *darkened area*. Overlap is defined as the area under the curve, formed by taking the smaller value of the two activities at each time point. The 95 % bootstrap CIs of overlap estimates are indicated in *parentheses*. The *black dashed vertical lines* indicate the approximate times of sunrise (05:15) and sunset (17:30)

from 3000 to 6000 km<sup>2</sup>, and these lands should be managed with a priority on wild ungulate recovery and minimal human disturbance (see below). With the 4000 km<sup>2</sup> of protected land in Russia, the total reserve area will be 10,000 km<sup>2</sup>. This would be large enough to support 30–50 breeding tigers and 50–90 breeding leopards (Goodrich et al. 2010; Hebblewhite et al. 2011).

Phase II is to further increase the spatial extent of TLRP from 6000 to  $20,000 \text{ km}^2$  by incorporating the adjacent forested landscapes that are not fragmented by highways, railroads, and major townships (Hebblewhite et al. 2012). Habitat of this size would be large enough for the two felids to be viable and function as source populations.

Phase III is to further expand the reserve network by incorporating the two other major forested regions of China's Natural Forests Protection Program, the Lesser Xing'an Mountains and the Changbai Mountains. When the TLRP is fully implemented, the Amur tiger and leopard may well be on their way to resettlement in their historical range in NE China with sufficient habitat to ensure their long-term sustainability.

# Immediate actions needed

Our study provides evidence that tigers and leopards are returning to China, but several hurdles exist for their resettlement. The two felids are at crossroads as currently available habitat is fully occupied while dispersal into China is severely limited. To help the returning populations get out of the present predicament, immediate actions are needed to implement TLRP which must be integrated with regional sustainable development to achieve the dual goal of promoting conservation and improving human wellbeing. China has the responsibility and capacity to carry out such a program. The Natural Forest Protection Program and other forest restoration projects initiated in recent years are important, but not sufficient. Specifically, we suggest the following immediate actions:

 To establish a "Special Ecological Zone" for protecting tigers and leopards, which is privileged with a unique set of policies and provides the institutional basis for TLRP;

- (2) To completely ban cattle grazing and human disturbances immediately within the reserve and eventually throughout the TLRP, with an incentive program established to encourage a shift from livestock herding to other livelihood opportunities;
- (3) To implement an ecosystem services-centered economic development model that promotes ecological tourism and conservation-related enterprises that directly benefit local people;
- (4) To establish an effective multi-target evaluation system, which consider both wildlife-focused and socioeconomic issues following the recommendations of the IUCN Reintroduction Specialist Group (http://www.iucnsscrsg.org);
- (5) To optimize land use pattern to maximize habitat connectivity and minimize human-wild-life conflicts;
- (6) To restore viable populations of large-bodied deer and wild boar throughout the region by removing snares and enhancing existing populations and relocation of wild animals as necessary;
- (7) To promote governmental cooperation between China and Russia to ensure establishing a binational conservation region within the next several years.

These actions must be taken timely and effectively if a viable future of the Amur tigers and leopards is to be ensured.

# Conclusion

For the first time, we provide comprehensive and direct evidence documenting the exact number of Amur tigers and leopards in China, as well as their spatial movements in great details. We find that both species are returning to China in large numbers, but resettlement is unlikely because of cattle grazing, human disturbances and large-sized deer absence. These hurdles can be removed through regional conservation planning, but actions must be taken now. Our study substantially improves our understanding of the current situation of the Amur tigers and leopards, and provides an evidence-based landscape conservation plan that will greatly enhance the longterm sustainability of these two species. Acknowledgments We sincerely thank Somphot Duangchantrasiri and Saksit Simcharoen for their great help with verifying the identities of tiger and leopard individuals. We also thank the State Forestry Administration, Jilin Province Forestry Bureau, and the Forestry Industry Bureau of Heilongjiang Province for field assistance. This work was supported by grants from the National Natural Science Foundation of China (31210103911, 31270567, 31421063, 31200410, 31470566 and 31300458) and the National Scientific and Technical Foundation Project of China (2012FY112000).

# References

- Ahearn SC, Smith JLD, Joshi AR, Ding J (2001) TIGMOD: an individual-based spatially explicit model for simulating tiger/human interaction in multiple use forests. Ecol Model 140(1–2):81–97
- Barlow ACD, McDougal C, Smith JLD, Gurung B, Bhatta SR, Kumal S, Mahato B, Tamang DB (2009) Temporal variation in tiger (*Panthera tigris*) populations and its implications for monitoring. J Mammal 90(2):472–478
- Carroll C, Miquelle DG (2006) Spatial viability analysis of Amur tiger *Panthera tigris altaica* in the Russian Far East: the role of protected areas and landscape matrix in population persistence. J Appl Ecol 43(6):1056–1068
- Dave C, Jhala Y (2011) Is competition with livestock detrimental for native wild ungulates? A case study of chital (*Axis axis*) in Gir Forest, India. J Trop Ecol 27:239–247
- Feng LM, Wang TM, Mou P, Kou XJ, Ge JP (2011) First image of an Amur leopard recorded in China. Cat News 55(Autumn):9
- Gilbert M, Miquelle DG, Goodrich JM, Reeve R, Cleaveland S, Matthews L, Joly DO (2014) Estimating the potential impact of canine distemper virus on the Amur tiger population (*Panthera tigris altaica*) in Russia. PLoS One 9(10):e110811
- Goodrich JM, Miquelle DG, Smirnov EN, Kerley LL, Quigley HB, Hornocker MG (2010) Spatial structure of Amur (Siberian) tigers (*Panthera tigris altaica*) on Sikhote-Alin Biosphere Zapovednik, Russia. J Mammal 91(3):737–748
- Guo Q, Brown JH, Enquist BJ (1998) Using constraint lines to characterize plant performance. Oikos 83(2):237–245
- Gurung B, Smith JLD, McDougal C, Karki JB, Barlow A (2008) Factors associated with human-killing tigers in Chitwan National Park, Nepal. Biol Conserv 141(12):3069–3078
- Hayward MW, Jedrzejewski W, Jedrzewska B (2012) Prey preferences of the tiger Panthera tigris. J Zool 286(3):221–231
- Hebblewhite M, Miguelle DG, Murzin AA, Aramilev VV, Pikunov DG (2011) Predicting potential habitat and population size for reintroduction of the Far Eastern leopards in the Russian Far East. Biol Conserv 144(10):2403–2413
- Hebblewhite M, Zimmermann F, Li Z, Miquelle DG, Zhang M, Sun H, Mörschel F, Wu Z, Sheng L, Purekhovsky A, Chunquan Z (2012) Is there a future for Amur tigers in a restored tiger conservation landscape in Northeast China? Anim Conserv 15(6):579–592
- Hebblewhite M, Miquelle DG, Robinson H, Pikunov DG, Dunishenko YM, Aramilev VV, Nikolaev IG, Salkina GP, Seryodkin IV, Gaponov VV, Litvinov MN, Kostyria AV,

Fomenko PV, Murzin AA et al (2014) Including biotic interactions with ungulate prey and humans improves habitat conservation modeling for endangered Amur tigers in the Russian Far East. Biol Conserv 178:50–64

- Henry P, Miquelle D, Sugimoto T, McCullough DR, Caccone A, Russello MA (2009) In situ population structure and ex situ representation of the endangered Amur tiger. Mol Ecol 18(15):3173–3184
- Horning M (2012) Constraint lines and performance envelopes in behavioral physiology: the case of the aerobic dive limit. Front Physiol 3:1–9
- Jiang GS, Sun HY, Lang JM, Yang LJ, Li C, Lyet A, Long B, Miquelle DG, Zhang CZ, Aramilev S, Ma JZ, Zhang MH (2014) Effects of environmental and anthropogenic drivers on Amur tiger distribution in northeastern China. Ecol Res 29(5):801–813
- Jilin Statistical Bureau (2013) Jilin statistical yearbook (in Chinese). China Statistics Press, Beijing
- Johnson A, Vongkhamheng C, Hedemark M, Saithongdam T (2006) Effects of human-carnivore conflict on tiger (*Pan-thera tigris*) and prey populations in Lao PDR. Anim Conserv 9(4):421–430
- Jutzeler E, Wu ZG, Liu WS, Breitenmoser U (2010) Leopard. Cat News 5(Autumn):30–33
- Kenney J, Allendorf FW, McDougal C, Smith JLD (2014) How much gene flow is needed to avoid inbreeding depression in wild tiger populations? P R Soc B 281(1789):20133337
- Kerley LL, Mukhacheva AS, Matyukhina DS, Salmanova E, Salkina GP, Miquelle DG (2015) A comparison of food habits and prey preference of Amur tiger (*Panthera tigris altaica*) at three sites in the Russian Far East. Integr Zool 10(4):354–364
- Li ZW, Wu JG, Kou XJ, Tian Y, Wang TM, Mu P, Ge JP (2009) Land use pattern and its dynamics changes in Amur tiger distribution region. Chin J Appl Ecol 20(3):713–724 (in Chinese)
- Madhusudan MD (2004) Recovery of wild large herbivores following livestock decline in a tropical Indian wildlife reserve. J Appl Ecol 41(5):858–869
- Miquelle DG, Smirnov EN, Quigley HB, Hornocker MG (1996) Food habits of Amur tigers in the Sikhote-Alin Zapovednik and the Russian Far East, and implications for conservation. J Wildl Res 1:138–147
- Miquelle DG, Pikunov DG, Dunishenko YM, Aramilev VV, Nikolaev IG, Smirnov EN, Salkina GP, Seryodkin IV, Gapanov VV, Fomenko PV, Litvinov MN, Kostyria AV, Korkisko VG, Murzin AA (2006) A survey of Amur (Siberian) tigers in the Russian Far East, 2004–2005. Final Report to the Save the Tiger Fund. Wildlife Conservation Society, New York, p. 77
- Miquelle DG, Goodrich JM, Kerley LL, Pikunov DG, Dunishenko YM, Aramiliev VV, Nikolaev IG, Smirnov EN, Salkina GP, Endi Z, Seryodkin IV, Carroll C, Gapanov VV, Fomenko PV, Kostyria AV, Murzin AA, Quigley HB, Hornocker MG (2010a) Science-based conservation of Amur tigers in the Russian Far East and Northeast China. In: Tilson R, Nyhus PJ (eds) Tiger of the world. The science, politics, and conservation of *Panthera tigris*, 2nd edn. Elsevier Limited, Oxford, pp 403–423
- Miquelle DG, Goodrich JM, Smirnov EN, Stephens PA, Zaumyslova OY, Chapron G, Kerley L, Murzin AA,

Hornocker MG, Quigley HB (2010b) The Amur tiger: a case study of living on the edge. In: Macdonald DW, Loveridge AJ (eds) Biology and conservation of wild felids. Oxford University Press, Oxford, pp 325–339

- O'Brien TG, Kinnaird MF, Wibisono HT (2003) Crouching tigers, hidden prey: Sumatran tiger and prey populations in a tropical forest landscape. Anim Conserv 6:131–139
- Pikunov DG, Miquelle DG, Abramov VK, Nikolaev IG, Seredkin IV, Murzin AA, Korkishko VG (2003) A survey of Far Eastern leopard and Amur tiger populations in Southwest Primorski Krai, Russian Far East (February 2003). Pacific Institute of Geography (FEB RAS), Wildlife Conservation Society, and Tigris Foundation, Vladivostok
- Pikunov DG, Seredkin IV, Aramilev VV, Nikolaev IG, Murzin AA (2009) Numbers of Far Eastern Leopards (*Panthera pardus orientalis*) and Amur Tigers (*Panthera tigris altaica*) in Southwest Primorski Krai, Russian Far East, 2007. Dalnauka, Vladivostok
- Ridout MS, Linkie M (2009) Estimating overlap of daily activity patterns from camera trap data. J Agric Biol Environ Stat 14(3):322–337
- Simcharoen A, Savini T, Gale GA, Simcharoen S, Duangchantrasiri S, Pakpien S, Smith JLD (2014) Female tiger *Panthera tigris* home range size and prey abundance: important metrics for management. Oryx 48(3):370–377
- Smith JLD, McDougal CW, Sunquist ME (1987) Female land tenure system in tigers. In: Tilson RL, Seal US (eds) Tigers of the world: the biology, biopolitics, management and conservation of an endangered species. Noyes Publications, Park Ridge, pp 97–108
- Soh YH, Carrasco LR, Miquelle DG, Jiang J, Yang J, Stokes EJ, Tang J, Kang A, Liu P, Rao M (2014) Spatial correlates of livestock depredation by Amur tigers in Hunchun, China: relevance of prey density and implications for protected area management. Biol Conserv 169:117–127
- Stewart KM, Bowyer RT, Kie JG, Cimon NJ, Johnson BK (2002) Temporospatial distributions of elk, mule deer, and cattle: resource partitioning and competitive displacement. J Mammal 83(1):229–244
- Sugimoto T, Nagata J, Aramilev VV, McCullough DR (2012) Population size estimation of Amur tigers in Russian Far East using noninvasive genetic samples. J Mammal 93(1):93–101

- Sugimoto T, Aramilev VV, Kerley LL, Nagata J, Miquelle DG, McCullough DR (2014) Noninvasive genetic analyses for estimating population size and genetic diversity of the remaining Far Eastern leopard (*Panthera pardus orientalis*) population. Conserv Genet 15(3):521–532
- Thomson JD, Weiblen G, Thomson BA, Alfaro S, Legendre P (1996) Untangling multiple factors in spatial distributions: lilies, gophers, and rocks. Ecology 77(6):1698–1715
- Tian Y, Wu JG, Kou XJ, Li ZW, Wang TM, Mou P, Ge JP (2009) Spatiotemporal pattern and major causes of the Amur tiger population dynamics. Biol Sci 17(3):211–225 (in Chinese)
- Tian Y, Wu JG, Smith AT, Wang TM, Kou XJ, Ge JP (2011) Population viability of the Siberian tiger in a changing landscape: going, going and gone? Ecol Model 222(17):3166–3180
- Tian Y, Wu JG, Wang TM, Ge JP (2014) Climate change and landscape fragmentation jeopardize the population viability of the Siberian tiger (*Panthera tigris altaica*). Landscape Ecol 29(4):621–637
- Uphyrkina O, Miquelle D, Quigley H, Driscoll C, O'Brien SJ (2002) Conservation genetics of the Far Eastern leopard (*Panthera pardus orientalis*). J Hered 93(5):303–311
- Wang TM, Yang HT, Xiao WH, Feng LM, Mou P, Ge JP (2014) Camera traps reveal Amur tiger breeding in NE China. Cat News 61(Autumn):18–19
- Wei YW, Yu DP, Lewis BJ, Zhou L, Zhou W, Fang X, Zhao W, Wu S, Dai L (2014) Forest carbon storage and tree carbon pool dynamics under natural forest protection program in northeastern China. Chin Geogr Sci 24(4):397–405
- Xiao WH, Feng LM, Zhao XD, Yang HT, Dou HL, Cheng YC, Mou P, Wang TM, Ge JP (2014) Distribution and abundance of Amur tiger, Amur leopard and their ungulate preys in Hunchun National Nature Reserve, Jilin. Biodiver Sci 22(6):717–724 (in Chinese)
- Young TP, Palmer TM, Gadd ME (2005) Competition and compensation among cattle, zebras, and elephants in a semi-arid savanna in Laikipia, Kenya. Biol Conserv 122(2):351–359
- Zhou SC, Sun HY, Zhang MH, Lu XD, Yang J, Li L (2008) Regional distribution and population size fluctuation fo wild Amur tiger (*Panthera tigris altaica*) in Heilongjiang Province. Acta Theriol Sin 28(2):165–173 (in Chinese)