BioOne COMPLETE

Does prey density limit Amur tiger Panthera tigris altaica recovery in northeastern China?

Authors: Zhang, Changzhi, Zhang, Minghai, and Stott, Philip

Source: Wildlife Biology, 19(4) : 452-461

Published By: Nordic Board for Wildlife Research

URL: https://doi.org/10.2981/12-090

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Downloaded From: https://complete.bioone.org/journals/Wildlife-Biology on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

Wildl. Biol. 19: 452-461 (2013)
DOI: 10.2981/12-090
© Wildlife Biology, NKV
www.wildlifebiology.com

Original article

Does prey density limit Amur tiger *Panthera tigris altaica* recovery in northeastern China?

Changzhi Zhang, Minghai Zhang & Philip Stott

A residual population of Amur tigers *Panthera tigris altaica* probably survives in the eastern Wanda Mountains (EWM) in China, where the main prey species are red deer *Cervus elaphus*, eastern roe deer *Capreolus pygargus* and wild boar *Sus scrofa ussuricus*. We used 53 snow sample plots each containing about 29 km of transects to detect ungulate presence and determined their total density in EWM in 2002 to be 87.9 ± 8.9 kg km^{-2}. We then applied these data to three published models that predict the relationship between tiger density and prey biomass density to obtain three estimates of tiger carrying capacity in EWM. Existing estimates of tiger density suggest that tigers were below carrying capacity estimates. Relationships between prey density and tiger density from 15 studies indicate a threshold prey biomass of 195 kg km^{-2} (CI: 33-433), below which a tiger population cannot be sustained. We therefore concluded that the EWM population of tigers is in peril. We compared densities between the years 2002 and 2008 using comparable data and found that the EWM populations of the three ungulate prey species all experienced decreases of 40-45%, apparently due to intense poaching. This rapid decline in prey density and pervasive threats to tigers and their prey in the EWM demands immediate and effective protection of ungulate and tiger populations from poaching if tigers are to persist and recover.

Key words: Amur tiger, Capreolus pygargus, carrying capacity, Cervus elaphus, Panthera tigris altaica, poaching, red deer, roe deer, Sus scrofa ussuricus, wild boar

Changzhi Zhang & Minghai Zhang, Northeast Forestry University, College of Wildlife Resources, 26 Hexing Road, Harbin 150040, People's Republic of China - e-mail addresses: amurtiger@126.com (Changzhi Zhang); zhangminghai2004@126.com (Minghai Zhang)
Philip Stott, University of Adelaide, School of Animal and Veterinary Sciences, Roseworthy Campus, Roseworthy, South Australia 5371, Australia - e-mail: philip.stott@adelaide.edu.au

Corresponding author: Minghai Zhang

Received 25 August 2012, accepted 14 July 2013

Associate Editor: R.J. Gutiérrez

The Amur tiger *Panthera tigris altaica* has been classified as Endangered by the International Union for Conservation of Nature (IUCN; Chundawat et al. 2011), and is also a 1st class Protected Wildlife species in China (Wang 1998). In 2005, 430-502 adult or subadult Amur tigers were estimated to live in Russia (Miquelle et al. 2007), with perhaps < 20 tigers surviving in China (Li et al. 2001, Yu et al. 2000) and few or none in Korea (Miquelle & Pikunov 2003, Miquelle et al. 2007). Currently, Amur tigers occur at two locations in China: in the Changbaishan Mountains (Miquelle et al. 2010, Li et al. 2010) and in the eastern Wanda Mountains (EWM; Zhang et al. 2005), where a tiger cub was found in 2010, which indicated the presence of at least one reproducing female.

Large carnivores like tigers can influence the structure of ungulate communities (Karanth et al. 2004), and hence, they may play a pivotal role in maintaining natural ecosystem functions (Sanderson et al. 2006). Concern over the failure of the wild tiger population in northeastern China and elsewhere to recover has generated calls for effective tiger conservation, culminating in the St. Petersburg Declaration, signed by the Heads of Government of the 13 tiger-range countries in November 2010 (Wikramanayake et al. 2011).

Changes in tiger numbers are the ultimate metric in

Downloaded From: https://complete.bioone.org/journals/Wildlife-Biology on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

assessing the effectiveness of conservation strategies to recover tiger populations. Although there are many methods for monitoring tiger populations, efforts to detect trends in populations with extremely few individuals, such as in northeastern China, can be difficult. In such a situation, monitoring trends in prey levels (Wang 2010) may facilitate assessments of the success of management interventions, because prey depletion is a common threat to tiger populations (Karanth & Stith 1999, Seidensticker 1986). Prey scarcity can affect felids by decreasing the proportion of reproductively active females, delaying the age of first reproduction, reducing litter size, increasing offspring and adult mortalities, increasing home-range size and increasing the numbers of transients and dispersing individuals, all of which are parameters affecting the demographic viability of populations (Fuller & Sievert 2001). One way to determine whether prey scarcity is a factor limiting Amur tiger recovery is to predict how many tigers could theoretically be maintained within an area with a measured prey biomass in order to estimate minimum thresholds for prey abundance (Khorozyan et al. 2008).

Deer (Cervidae) species and wild boar *Sus scrofa* are the main prey of the tiger (Stöen & Wegge 1996), but they are difficult to survey using direct counts if detection probability is low, as is the case in northeastern China. However, at higher latitudes, ungulate tracks can be detected in snow (Ma et al. 2001), which in our area lasts for up to five months each year (Wei et al. 2011), and thus allows relative estimates of ungulate abundance to be determined. Absolute densities can be derived from such indices if suitable correction factors are available (Schwarz & Seber 1999).

In the Sikhote-Alin State Biosphere Zapovednik (SABZ) in the Russian Far East and elsewhere in Russia, the Formozov-Malyshev-Pereleshin (FMP) formula has been used to estimate abundances of large mammals (Stephens et al. 2006). However, the FMP requires knowledge of the mean daily distances moved by individuals and the factors affecting daily travel distances, which are not known for these species in northeastern China, although limited data are available for deer in SABZ. An alternative is the traditional Chinese strip-transect method, but its precision is diminished by uncertainty about the width of the strip and the accuracy of the conversion coefficient, which relates the number of tracks to the number of individual ungulates (Piao et al. 1995).

The aims of our study are to quantify ungulate density in EWM, to use previously published formulae and data derived elsewhere to estimate tiger carrying capacity of the EWM, and to compare our estimates of carrying capacity with records of tiger numbers and prey determined using direct surveys. We used the Sun et al. (1999) sample-plot method for estimating ungulate densities. Based on our estimates, we make recommendations for tiger conservation in the EWM.

Material and methods

Study area

Our study was conducted in a 5,393 km^2 area of the eastern Wanda Mountains, China (45°57'-47°05'N; 132°29'-133°57'E; Fig. 1), representing 78% of the land managed by the Dong Fanghong and Yingchun Forestry Bureaus. The climate is characterised by long cold winters and short hot summers. The annual average temperature is 2.2°C, and average extreme temperatures range between -34.8 and +34.6°C. The frost-free period lasts 120 days, from late April to late September. Average annual precipitation ranges between 500 and 800 mm and is concentrated in summer. At lower altitudes, the vegetation is deciduous forest with an overstory of Japanese white birch *Betula platyphylla*, poplar *Populus davidiana*, Mongolian oak *Quercus mongolica* and Manchurian ash *Fraxinus mandshurica*, whereas at higher altitudes, it is a mixed coniferous-deciduous forest with an overstory of Korean pine *Pinus koraiensis*, Amur basswood *Tilia amurensis*, yellow birch *B. dahurica* and painted maple *Acer mono*. Ungulates occuring in the EWM are wild boar *Sus scrofa ussuricus*, red deer *Cervus elaphus*, eastern roe deer *Capreolus pygargus*, musk deer *Mochus moschiferus* and ghoral *Nemorhaedus caudatus*. Sika deer *Cervus nippon* and moose *Alces alces cameloides* no longer occur in the EWM, nor does the Amur leopard *Panthera pardus orientalis*. The Eurasian lynx *Lynx lynx* is present but at a very low density.

Estimation of prey density and abundance

Attempts to relate the density of a predator to the biomass of all available prey (e.g. Kawanishi & Sunquist 2004) or of preferred prey (Kiffner et al. 2009) suggested that the biomass of important prey species would allow more robust estimates of an area's carrying capacity for a predator. We therefore estimated the density and abundance of red deer, roe deer and wild boar in the EWM. We focused on these

Downloaded From: https://complete.bioone.org/journals/Wildlife-Biology on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

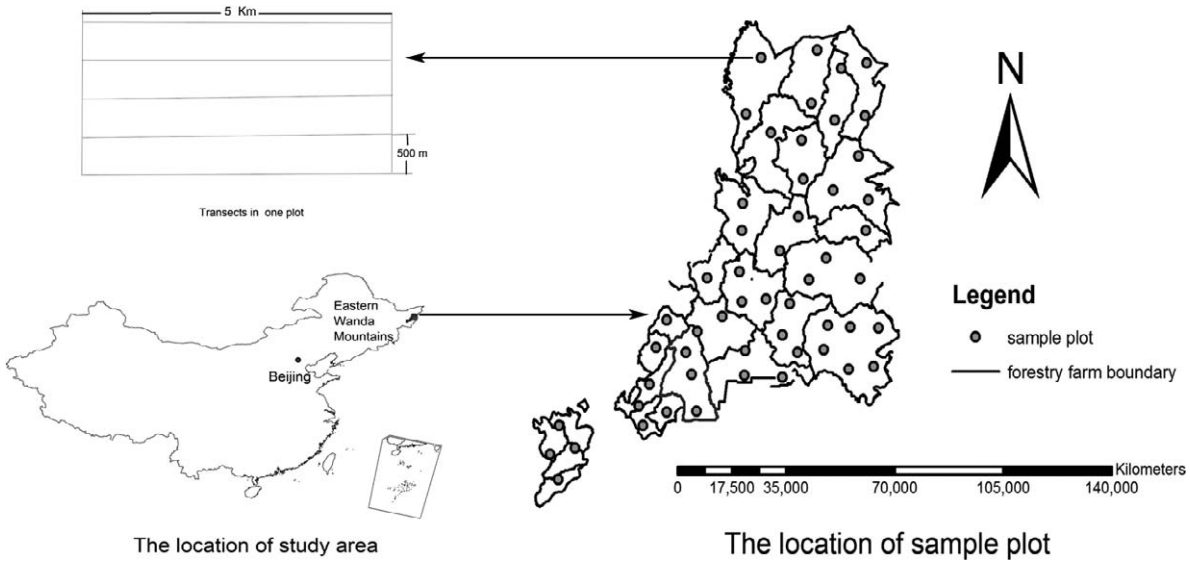


Figure 1. Location of eastern Wanda Mountains in China and the distribution of the survey plots within the forestry farms. The design of the survey plots is shown.

three species because they were shown by Miquelle et al. (1996) to be the most common prey (together representing 90.1% of all kills) of the Amur tiger in the SABZ. We did not count livestock because there were few livestock killed by tiger; our monitoring data showed that about one cattle and one dog was depredated every two years by tigers from 2000 to 2010 in the EWM (C.Z. Zhang & M.H. Zhang, unpubl. data). We used two methods (Carbone & Gittleman 2002, Miquelle et al. 1999) to estimate prey biomass, and in addition, we estimated density and abundance in numerical terms using ungulate survey protocols in general use in northeastern China (Sun 2011).

To survey ungulate density, we delineated habitat types in advance using existing maps of topography, vegetation and history of forest management (as an indicator of successional stage) to create layers in ArcGIS 9.3 (ESRI 2008). We then used 10 km^2 plots to survey ungulate density. To maintain a homogeneous sampling effort over the study area, we surveyed ca 10% of the study area by assigning one to six survey plots to each forestry farm based on the relative size of each forestry farm, resulting in a total of 53 plots. These plots were also evenly distributed among habitat types in proportion to their relative coverage of the study area. Within those constraints, we randomly selected sites and orientations of the survey plots; any plot that was not completely covered in snow was discarded and a replacement plot was randomly selected. As designed, each survey plot contained five parallel transect lines each 5 km long and 500 m apart, together with two perpendicular transect lines joining the ends of the other lines (see Fig. 1), creating four sectors in each plot.

Personnel involved in the surveys were either forest guards or members of the College of Wildlife Resource, Northeast Forestry University, and had undergone training in species identification based on Ma et al. (2001) data collection protocols. Each data collector had at least three years of field experience in ungulate surveys. The personnel were divided into teams of five with each team undertaking the survey of one plot in each working day. Each plot was only surveyed once, and no survey was undertaken if snow had fallen in the previous 24 hours. The transect lines were surveyed on foot, with the team assembling as a group at the mid-point of one of the end transects. Each member of the team surveyed one of the 5-km long transects, and the individuals responsible for the outer transects also surveyed half of each perpendicular transect as they moved to and from their 5-km transect. Each member carried a GPS unit to record the actual route taken, and calculations were based on actual plot areas, not on the design of the plots. When tracks assessed as < 24 hours old were found crossing a transect line, the surveyor recorded the species, the group size and whether the individual or group moved into or out of the plot sector. Animals of the same species were regarded as being in the same

Downloaded From: https://complete.bioone.org/journals/Wildlife-Biology on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

group if tracks of equal freshness were within 30 m of each other and travelling in the same direction.

The method was based on several assumptions: that 1) the plots accurately represented the relative proportions of the various habitat types in the study area as a whole, 2) every individual ungulate would cross at least one transect line within the 24-hour period prior to the survey 3) the size of any groups of ungulates would remain constant over the 24-hour period, 4) that animals would not cross the external boundaries of a plot in response to disturbance caused by the personnel, 5) that the personnel could accurately distinguish ungulates to species based on their tracks and 6) that personnel could accurately distinguish between tracks $<$ 24 hours old and tracks $>$ 24 hours old.

For each species, the number of individuals within a plot sector at the time of the survey was determined by subtracting the number of groups of each size category (1, 2, 3, ...N) leaving the sector in a 24-hour period from the number of groups of that size class entering the sector during that period multiplied by that group size, and adding the outcome for each group size category. The number in the plot as a whole was determined by adding the results from each sector, and the density was calculated using that total and the actual area as determined by applying ArcGIS 9.3 to the GPS records. The density in any particular habitat type was mean density of the survey plots within that habitat type, and the density in the study area was taken as the mean density of the habitat type layers weighted according to the proportion of that layer in the study area as a whole as determined using ArcGIS 9.3.

Data on prey density were converted to biomass km^{-2} using published adult female body weights for northeastern China (red deer: 150 kg; roe deer: 30 kg; wild boar: 120 kg; Liu 2006, Ma 1986, Zhou & Zhang 2011). To account for the proportion of subadults in the prey population, we corrected the biomass by a factor of 0.75, following Schaller (1972). We compared prey density between 2002 and 2008 using data for EWM and prey density in 2008 was derived from Zhou & Zhang (2011).

Estimations of carrying capacity for tigers based on prey densities

First, we estimated tiger carrying capacity based on Carbone & Gittleman's (2002) model predicting carnivore numbers based on available prey biomass for 25 carnivores (including the tiger) ranging in body weight from 0.14 to 310 kg. This model predicts that 10,000 kg of prey supports ~ 90 kg of a given species of carnivore irrespective of body mass. We assumed that the Eurasian lynx predated almost exclusively on roe deer, and that their impact on prey biomass was minimal. From this rule, we derived the following function as our first model:

$$T_1 = (P_b{*}90{*}100)/(BW_t{*}10,000), \quad \text{or}$$
$$T_1 = 0.9{*}P_b/BW_t,$$

where T_1 is the number of tigers/100 km^2, P_b is the ungulate biomass (kg/km^2) and BW_t is the mean tiger body weight (kg).

Secondly, we estimated tiger carrying capacity using Karanth et al.'s (2004) simple two-parameter, one-variable (prey abundance) model:

$$T_2 = A{*}P_n^b,$$

where T_2 is the number of tigers/unit area, P_n is the number of prey animals in the same area, A is the proportion of the prey population killed by tigers in a year and the exponent b ($\leq$ 1.0) allows for a non-linear relationship between prey numbers and tiger numbers. Based on field data from tigers in India, Karanth et al. (2004) assessed b as 0.514, but we have followed Treves et al. (2009), who applied the same model to lions in central Africa and proposed that b reflects metabolic scaling factors such as the energetic efficiency with which prey can be converted to predator, and we therefore estimated b to be 0.725, the median of published metabolic weight exponents (0.67-0.78; McNab 1989, White & Seymour 2005, Carbone et al. 2007). For A, Karanth et al. (2004) divided the number of prey killed by each tiger annually (50) by the proportion of available prey tigers annually removed (10%), but we express densities per 100 km^2 for tigers and per km^2 for prey so our second model is therefore:

$$T_2 = 0.2{*}P_d^{0.725},$$

where T_2 is the number of tigers/100 km^2 and P_d is the ungulate density (number of individuals/km^2).

Thirdly, we estimated tiger carrying capacity by applying Miquelle et al.'s (1999) formula, derived from their review of tiger densities and prey biomass densities at four sites. The formula is:

$$P_b = -256.3 + 476.5{*}T_3, \quad \text{or}$$
$$T_3 = (P_b + 256.3)/476.5,$$

where T_3 is the number of tigers/100 km^2 and P_b is the prey biomass (kg/km^2).

Downloaded From: https://complete.bioone.org/journals/Wildlife-Biology on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

If there is any prey in the region, no matter how sparse, these three models will always yield a positive result. However, there is likely a point at which the energetic cost of searching a very large area will exceed the yield from a single kill. We sought a threshold effect by reviewing literature reporting both tiger density and the density of prey biomass, regressed tiger density as the dependent variable against Ln density of prey biomass as the independent variable, obtained the regression formula and used our data on ungulate biomass from our field survey in EWM to estimate the tiger carrying capacity in the region (T_4; individuals/100 km^2). Our fourth model is therefore:

$$T_4 = A*LnP_b + C,$$

where T_4 is the tiger density (individuals/100 km^2), P_b is the prey biomass (kg/km^2), A is the slope of the regression and C is the y intercept.

Data were available from 15 areas (Table 1), but for some areas, data were recalculated to make it comparable. In each case, we assumed that the relationship between tiger density and prey density was not distorted by anthropogenic influences. We calculated the density estimates for the Royal Chitwan National Park based on the data on home range and social organisation reported by Sunquist (1981), yielding tiger density estimates of 5.8-8.7 tigers/100 km^2. For these data, and for the range of 0.6-1.4 tigers reported per 100 km^2 in SABZ by Miquelle et al. (1999), we used the mean of the range. Cubs < 1 year old were not included from the camera-trapping data on tiger density for all 13 of the other sites, but Karanth & Stith (1999) suggest that cubs may form 25% of a normal tiger population. We relied on this percentage to estimate total tiger densities for these 13 sites.

Direct estimations of tiger abundance

Sun et al. (1999) and Zhou et al. (2008) estimated 4-5 tigers in EWM in 1999 and 2008, respectively. We assumed that the number present in the winter of 2002/03 was also 4-5, and therefore that the density was 0.076-0.095 tigers 100 km^{-2}.

Results

Estimation of prey density and abundance

In the 53 snow sample plots, 1,545.62 km of transects were surveyed, and 452 red deer, 1,245 roe deer and 827 wild boar tracks < 24 hours old were recorded. We calculated densities of red deer (0.2010 ± 0.0270 km^{-2}), roe deer (0.4980 ± 0.0436 km^{-2}) and wild boar (0.3423 ± 0.0275 km^{-2}). Converting these density estimates to biomass, we calculated total ungulate biomass to be 87.9 ± 8.9 kg km^{-2}.

Table 1. Tiger density and Ln (preferred ungulate biomass) from selected national parks (NP) and reserves in Asia.

Site	Country	Tiger density N 100 km^{-1}	Ln	Source
Kaziranga NP	India	22.40	8.33	Karanth & Stith 1999
Bandipur NP	India	16.00	8.61	Karanth & Nichols 2000
Kanha NP	India	15.60	8.19	Karanth & Stith 1999
Nagarahole NP	India	15.33	8.57	Karanth & Stith 1999
Ranthambhore NP	India	15.28	8.65	Karanth & Nichols 2000
Royal Chitawan NP	Nepal	7.25	7.07	Sunquist 1981
Rajaji NP	India	6.83	8.48	Harihar et al. 2009
Pench NP	India	5.47	8.58	Karanth & Stith 1999
Bhadra NP	India	4.56	7.54	Karanth & Nichols 2000
Merapoh, Taman Negara NP	Malaysia	2.64	5.78	Kawanishi & Sunquist 2004
Kuala Koh,Taman Negara NP	Malaysia	2.48	5.54	Kawanishi & Sunquist 2004
Bukit Barisan Selatan NP	Indonesia	2.08	5.98	O'Brien et al. 2003
Kuala Terengan, Taman Negara NP	Malaysia	1.47	5.29	Kawanishi & Sunquist 2004
Sikhote-Alin Zapovednik	Russia	1.00	5.72	prey; Stephens et al. 2006 tiger; Miquelle et al. 1999
Jigme Singye Wangchuck NP	Bhutan	0.69	5.78	prey; Wang & Macdonald 2009a tiger density; Wang & Macdonald 2009b

Ungulate body weight from Schaller 1967, Karanth & Sunquist 1992, Medway 1978, Reddy et al. 2004, Seidensticker 1976, Tamang 1979, Prater 1971, Eisenberg & Seidensticker 1976, Karanth & Sunquist 1992, Bagchi et al. 2003.

Downloaded From: https://complete.bioone.org/journals/Wildlife-Biology on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

Table 2. Tiger carrying capacity in the eastern Wanda Mountains estimated by three methods (T_1, T_2 and T_3) based on available biomass of ungulate prey.

	Method; mean (95% confidence intervals)		
	T_1 Carbone & Gittleman (2002)	T_2 Karanth et al. (2004)	T_3 Miquelle et al. (1999)
Tiger capacity 100 km^{-2}	0.395 (0.356-0.435)	0.206 (0.192-0.220)	0.676 (0.662-0.690)

Estimates of carrying capacity based on prey densities

Estimates of tiger carrying capacity in EWM based on available biomass of ungulate prey varied from 0.20 to 0.67 tigers/100 km^2 (Table 2).

There was a significant relationship between tiger density and Ln transformed ungulate biomass ($F = 22.25$, $N = 15$, $P = 0.0004$, $R^2 = 0.6312$; Fig. 2). The relationship is described by:

$$T_4 = 4.101 * \mathrm{Ln}(P_b) - 21.63,$$

where P_b is ungulate biomass in kg km^{-2} and T_4 is the supported tiger density in numbers of tigers per 100 km^{-2}. The P_b intercept when $T_4 = 0$ is at 195 (CI: 33-433) kg km^{-2}.

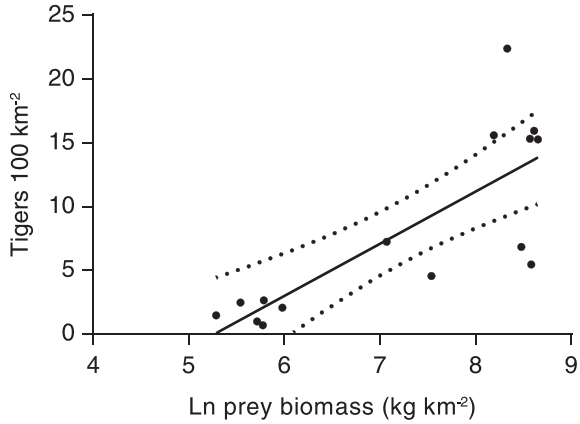


Figure 2. Relationship between tiger density and biomass of important ungulate prey for 15 areas in Asia. The relationship is described by the equation: tiger density = 4.1012 Ln (preferred ungulate biomass) - 21.626; $R^2 = 0.61507$.

Discussion

Estimates of the relationship between prey biomass and tiger density are fraught with uncertainty because tiger numbers may have been artificially depressed by poaching in some areas and because the impact of tigers on the prey populations would be confounded by the impact of any sympatric competing predator (Karanth et al. 2004). Because the Amur leopard is now extinct in the eastern Wanda Mountains and the Eurasian lynx is extremely rare, the tiger carrying capacity of the ungulate populations in the mountains could be 50% higher than estimates for Bengal tiger *P. t. tigris*, which is in broad sympatry with other large predators such as the Indian leopard *P. p. fusca* and the dhole *Cuon alpines* (Karanth et al. 2004). The Amur leopard is also not present in Sikhote-Alin Zapovednik, and so the estimate of carrying capacity using data from Miquelle et al. (1999) may more closely approximate the actual carrying capacity in the EWM. Nevertheless, even the carrying capacity estimated according to the Karanth et al. (2004) model (T_2, 10-11 tigers), was greater than the observed abundance (4-5 tigers; Zhou et al. 2008). The estimate based on the Carbone & Gittleman (2002) general carnivore model (T_1, 19-23 tigers) was also much higher than the direct measures.

Given that the estimates of carrying capacity (our study) were above the direct records of tiger abundance (Zhou et al. 2008) in the eastern Wanda Mountains, and given that tiger poaching and illegal killing are well-known problems across the range of the tiger, it might seem reasonable to conclude that our study provides indirect evidence of some adverse influence such as poaching acting directly on the tiger population. However, extrapolation of the regression of the relationships between tiger density and prey biomass at 15 sites suggested a threshold effect, with tiger density dropping to zero at a prey biomass of 195 kg km^{-2} (see Fig. 2). We calculated the 2002 prey biomass in EWM as 88 kg km^{-2}, which is below the mean but within the confidence interval of the regression.

During our field survey, we frequently encountered indications of the presence of poachers (e.g. camps, human tracks and snares). Subsistence poaching of red and roe deer and wild boar using cable snares and poison, supplemented by hunting with hounds for wild boar, is responsible for 88% of ungulate mortality in the Wanda Mountains as a whole (Zhou & Zhang 2011); the density of prey is therefore below carrying capacity, and much lower than densities reported for Sikhote-Alin Zapovednik in Russia (Stephens et al. 2006).

A population viability analysis has indicated that

Downloaded From: https://complete.bioone.org/journals/Wildlife-Biology on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

the Amur tiger is highly sensitive to prey scarcity (Tian et al. 2011). Felids respond to decreasing prey density by increasing foraging effort (Eurasian lynx; Schmidt 2008, Geoffroy's cat *Leopardus geoffroyi*; Pereira 2010) and are forced to travel longer distances with lower hunting success (Eurasian lynx; O'Donoghue et al. 1998), negatively impacting on their energy balance. As prey density declines, there should be a threshold at which point the increased energetic demands of hunting are not matched by the energy yield from the kills, leading ultimately to energy depletion and starvation. Such an outcome has been observed in response to an 88% reduction in the availability of European hares *Lepus europaeus* for Geoffroy's cat (Pereira 2010). López-Bao et al. (2010) concluded that a rabbit density of 50 km^{-2} was required to sustain Iberian lynx *Lynx pardinus*. Although the density of prey for the Amur tiger was within the confidence limits for tiger persistence in the EWM, it was below the calculated threshold in 2002, and more so in 2008.

We have made assumptions that must temper our conclusions. One assumption is that the deer and tiger populations at the 15 sites used for the regression analysis were all at equilibrium, but poaching of both ungulates (Jathanna et al. 2003) and tigers (Gopal et al. 2010), and the presence of competing carnivores such as the leopard (Karanth et al. 2004) means that the relationship between the tigers and the ungulates are confounded, and without human predation, prey density and carrying capacity for tigers would likely be greater (Karanth et al. 2004). To compare ungulate densities in EWM between 2002 and 2008, we assumed that the mean densities in the whole of the area that we surveyed and in the eastern portion of the area that was surveyed by Zhou et al. (2011) were the same, but the eastern portion subjectively appears to be a superior ungulate habitat. Also, the ungulate density-survey method traditionally used in China and Russia is based on distinguishing 24-hour old snow tracks from older tracks, but overnight refreezing obscures the distinction, adding an element of uncertainty to the counts. Although tracks made during morning crepuscular activity are readily distinguishable during the day (Ginsberg et al. 2002), we persisted with the traditional method to allow results to be compared between studies. The direct counts of tigers are also subject to underestimation because they rely on opportunistic findings by a network of observers (Smirnov & Miquelle 1999).

Conclusion

Poaching of tigers is generally considered to be a threat to the persistence of tigers (e.g. Miller et al. 2011), but Karanth & Stith (1999) and Karanth et al. (2004) have clearly demonstrated that prey depletion can be an equal threat. Therefore, poaching of the prey on which the tiger populations depend is as important as poaching of tigers themselves. We conclude that the tiger population in the eastern Wanda Mountains is in peril because the density of the prey species is below the threshold density necessary to support a tiger population. Intensive poaching of ungulates, evidenced by the frequency at which snares are found in the mountains, must be controlled if the tiger population is to survive.

Acknowledgements - our study was funded by the Rhinoceros and Tiger Conservation Fund (Agreement No. 98210-2-G191) and WWF Kathryn Fuller Science for Nature Fund for PhD of tiger research (Agreement No. RY08). We thank E. Zhang, T. Wang, and D. Miquelle (Wildlife Conservation Society), and D.G. Pikunov and I.G. Nikolaev (Russian Academy of Sciences), for help given throughout this project. In addition, we appreciate help from the staff of Heilongjiang General Bureau of Forest Industry and Heilongjiang Provincial Department, especially H. Dong. We also thank the professional staff, guides and drivers of Dong Fanghong Forest Bureau and Yingchun Forest Bureau. Finally, we thank Matt Hayward and an anonymous reviewer who provided thorough and thoughtful input that greatly improved our manuscript.

References

Bagchi, S., Goyal, S.P. & Sankar, K. 2003: Prey abundance and prey selection by tigers (*Panthera tigris*) in a semi-arid, dry deciduous forest in western India. - Journal of Zoology (London) 260: 285-290.

Carbone, C. & Gittleman, J.L. 2002: A common rule for the scaling of carnivore density. - Science 295: 2273-2276.

Carbone, C., Teacher, A. & Rowcliffe, J.M. 2007: The costs of carnivory. - Plos Biology 5: 363-368.

Chundawat, R.S., Habib, B., Karanth, U., Kawanishi, K., Ahmad Khan, J., Lynam, T., Miquelle, D., Nyhus, P., Sunarto, S., Tilson, R. & Wang, S. 2011: *Panthera tigris*. - In: IUCN 2012; IUCN Red List of Threatened Species. Version 2012.2. Available at: http:// www.iucnredlist.org (Last accessed on 4 May 2013).

Eisenberg, J.F. & Seidensticker, J. 1976: Ungulates in southern Asia: a consideration of biomass estimates for selected habitats. - Biological Conservation 10: 293-308.

ESRI 2008: ArcGis version 8.3 - ESRI, Redlands, California, USA.

Downloaded From: https://complete.bioone.org/journals/Wildlife-Biology on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

Fuller, T.K. & Sievert, P.R. 2001: Carnivore demography and the consequences of changes in prey availability. - In: Gittleman, J.L., Funk, S.M., Macdonald, D.W. & Wayne, R.K. (Eds.); Carnivore Conservation. Cambridge University Press, Cambridge, UK, pp. 163-178.

Ginsberg, J., Miquelle, D. & Zhang, E.D. 2002: Coordination of efforts to survey ungulate across the range of the Amur tiger - Final Report. - US Fisheries and Wildlife Service, 30 pp.

Gopal, R., Qureshi, Q., Bhardwaj, M., Singh, R.K.J. & Jhala, Y.V. 2010: Evaluating the status of the endangered tiger *Panthera tigris* and its prey in Panna Tiger Reserve, Madhya Pradesh, India. - Oryx 44: 383-389.

Harihar, A., Pandav, B. & Goyal, S.P. 2009: Responses of tiger (*Panthera tigris*) and their prey to removal of anthropogenic influences in Rajaji National Park, India. - European Journal of Wildlife Research 55: 97-105.

Jathanna, D., Karanth, K.U. & Johnsingh, A.J.T. 2003: Estimation of large herbivore densities in the tropical forests of southern India using distance sampling. - Journal of Zoology (London) 261: 285-290.

Karanth, K.U. & Nichols, J.D. 2000: Ecological status and conservation of tigers in India. Final technical report to the Division of International Conservation, US Fish and Wildlife Service, Washington, DC; Wildlife Conservation Society, New York; Center for Wildlife Studies, Bangalore, India. - US Fish and Wildlife Service, Washington, USA, 115 pp.

Karanth, K.U., Nichols, J.D., Kumar, N.S., Link, W.A. & Hines, J.E. 2004: Tigers and their prey: Predicting carnivore densities from prey abundance. - In: Orians, G.H. (Ed.); Proceedings of the National Academy of Sciences of the United States of America 101: 4854-4858.

Karanth, K.U. & Stith, B.M. 1999: Prey depletion as a critical determinant of tiger population viability. - In: Seidensticker, J., Christie, S. & Jackson, P. (Eds.); Riding the tiger: tiger conservation in human-dominated landscapes. Cambridge University Press, Cambridge, UK, pp. 100-113.

Karanth, K.U. & Sunquist, M.E. 1992: Population structure, density and biomass of large herbivores in the tropical forests of Nagarhole, India. - Journal of Tropical Ecology 8: 21-35.

Kawanishi, K. & Sunquist, M.E. 2004: Conservation status of tigers in a primary rainforest of peninsular Malaysia. - Biological Conservation 120: 329-344.

Khorozyan, I.G., Malkhasyan, A.G. & Abramov, A.V. 2008: Presence-absence surveys of prey and their use in predicting leopard (*Panthera pardus*) densities: a case study from Armenia. - Integrative Zoology 3: 322-332.

Kiffner, C., Meyer, B., Muhlenberg, M. & Waltert, M. 2009: Plenty of prey, few predators: what limits lions *Panthera leo* in Katavi National Park, western Tanzania? - Oryx 43: 52-59.

Li, T., Jiang, J.S., Wu, Z.G., Han, X.D., Wu, J.C. & Yang, X. 2001: Survey of Amur tiger in Jilin Province. (In Chinese with an English summary.) - Acta Theriologica Sinica 21: 1-6.

Li, Z., Zimmerman, F., Hebblewhite, M., Purekhovsky, A., Morschel, F., Chunquan, Z. & Miquelle, D. 2010: Study on the potential tiger habitat in the Changbaishan Area, China. - China Forestry Publishing House, Beijing, China, 88 pp.

Liu, Q.X. 2006: Population viability analysis of red deer in Wandashan Forestry Area. (In Chinese with an English summary.) - M.Sc. thesis, Northeast Forestry University, China, 59 pp.

López-Bao, J.V., Rodríguez, A. & Palomares, F. 2010: Abundance of wild prey modulates consumption of supplementary food in the Iberian lynx. - Biological Conservation 143: 1245-1249.

Ma, S.L., Ma, X.F. & Shi, W.Y. 2001: A guide to mammal tracking in China. - China Forestry Publishing House, Beijing, China, 270 pp. (In Chinese).

Ma, Y.Q. 1986: Mammals of Heilongjiang Province. - Science and Technology Press, China, 520 pp. (In Chinese).

McNab, B.K. 1989: Basal rate of metabolism, body size, and food habits in the Order Carnivora. - In: Gittleman, J.L. (Ed.); Carnivore behavior, ecology and evolution. Comstock Associates, Ithaca, New York, USA, pp. 335-354.

Medway, L. 1978: The wild mammals of Malaya (peninsular Malaysia) and Singapore. 2nd edition. - Oxford University Press, Petaling Jaya, Malaysia, 156 pp.

Miller, C.S., Petrunenko, Y.K., Goodrich, J.M., Hebblewhite, M., Seryodkin, I.V. & Miquelle, D.G. 2011: Translocation a success, but poaching remains a problem for Amur tigers. - Cat News 55: 22-25.

Miquelle, D.G., Goodrich, J.M., Kerley, Pikunov, L.L. Dunishenko, D.G. Yu, M., Aramiliev, V.V., Smirnov, E.N., Nikolaev, I.G., Salkina, G.P. Zhang, E., Seryodkin, I.V., Carroll, C., Gapanov, V.V., Fomenko, P.V., Kostyria, A.V., Murzin, A.A., Quigley, H.B. & Hornocker, M.G. 2010: Science-based conservation of Amur tigers in Russian Far East and Northeast China. - In: Tilson, R. & Nyhus, P. (Eds.); Tigers of the World. Noyes Press, New Jersey, USA, pp. 399-419.

Miquelle, D.G. & Pikunov, D.G. 2003: Status of the Amur tiger and far eastern leopard. - In: Newell, J.P. (Ed.); The Russian Far East: A reference guide for conservation and development. Daniel and Daniel Publishers, McKinleyville, California, USA, pp. 106-109.

Miquelle, D.G., Pikunov, D.G., Dunishenko, Y.M., Aramilev, V.V., Nikolaev, I.G., Abramov, V.K., Smirnov, E.N., Salkina, G.P., Seryodkin, I.V., Gaponov, V.V., Fomenko, P.V., Litvinov, M.N., Kostyria, A.V., Yudin, V.G., Korkishko, V.G. & Murzin, A.A. 2007: 2005 Amur tiger census. - Cat News 46: 14-16.

Miquelle, D.G., Smirnov, E.N., Merrill, T.W., Myslenkov, A.E., Quigley, H.B., Hornocker, M.G. & Schleyer, B. 1999: Hierarchical spatial analysis of Amur tiger relationships to habitat and prey. - In: Seidensticker, J., Christie, S.

Downloaded From: https://complete.bioone.org/journals/Wildlife-Biology on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

& Jackson, P. (Eds.); Riding the Tiger: Tiger conservation in human-dominated landscapes. Cambridge University Press, Cambridge, UK, pp. 71-99.

Miquelle, D.G., Smirnov, E.N., Quigley, H.G., Hornocker, M.G., Nikolaev, I.G. & Matyushkin, E.N. 1996: Food habits of Amur tigers in Sikhote-Alin Zapovednik and the Russian Far East, and implications for conservation. - Journal of Wildlife Research 1: 138-147.

O'Brien, T.G., Kinnaird, M.F. & Wibisono, H.T. 2003: Crouching tigers, hidden prey: Sumatran tiger and prey populations in a tropical forest landscape. - Animal Conservation 6: 131-139.

O'Donoghue, M., Boutin, S., Krebs, C.J., Zuleta, G., Murray, D.L. & Hofer, E.J. 1998: Functional responses of coyotes and lynx to the snowshoe hare cycle. - Ecology 79: 1193-1208.

Pereira, J.A. 2010: Activity pattern of Geoffroy's cats (*Leopardus geoffroyi*) during a period of food shortage. - Journal of Arid Environments 74: 1106-1109.

Piao, R., Guan, G. & Zhang, M. 1995: Population size and distribution of moose in China. - Acta Theriologica Sinica 15: 11-16. (In Chinese).

Prater, S.H. 1971: The book of Indian animals. 3rd edition. - Bombay Natural History Society, Bombay, India, 324 pp.

Reddy, H.S., Srinivasulu, C. & Rao, K.T. 2004: Prey selection by the Indian tiger (*Panthera tigris tigris*) in Nagarjunasagar Srisailam Tiger Reserve, India. - Mammalian Biology 69: 384-391.

Sanderson, E., Forrest, J., Loucks, C., Ginsberg, J., Dinerstein, E., Seidensticker, J., Leimgruber, P., Songer, M., Heydlauff, A., O'Brien, T., Bryja, G., Klenzendorf, S. & Wikramanayake, E. 2006: Setting priorities for the conservation and recovery of wild tigers: 2005-2015. The Technical Assessment. - WCS, WWF, Smithsonian Institute, and NFWF-STF., New York and Washington, USA, 50 pp.

Schaller, G.B. 1967: The Deer and the Tiger. - University of Chicago Press, Chicago, Illinois, USA, 370 pp.

Schaller, G.B. 1972: The Serengeti lion. - University of Chicago Press, Chicago, Illinois, USA, 480 pp.

Seidensticker, J. 1976: Ungulate populations in Chitawan Valley, Nepal. - Biological Conservation 10: 183-210.

Seidensticker, J. 1986: Large carnivores and the consequences of habitat insularization: ecology and conservation of tigers in Indonesia and Bangladesh. - In: Miller, S.D. & Everett, D.D. (Eds.); Cats of the world: biology, conservation and management. National Wildlife Federation, Washington, USA, 501 pp.

Schmidt, K. 2008: Behavioural and spatial adaptation of the Eurasian lynx to a decline in prey availability. - Acta Theriologica 53: 1-16.

Schwarz, C.J. & Seber, G.A.F. 1999: Estimating animal abundance: Review III. - Statistical Science 14: 427-456.

Smirnov, E.N. & Miquelle, D.G. 1999: Population dynamics of the Amur tiger in Sikhote-Alin State Biosphere Reserve. - In: Seidensticker, J., Christie, S. & Jackson, P. (Eds.); Riding the tiger: tiger conservation in human-dominated landscapes. Cambridge University Press, Cambridge, UK, pp. 61-70.

Stephens, P.A., Zaumyslova, O.Y., Miquelle, D.G., Myslenkov, A.I. & Hayward, G.D. 2006: Estimating population density from indirect sign: track counts and the Formozov-Malyshev-Pereleshin formula. - Animal Conservation 9: 339-348.

Stöen, O.G. & Wegge, P. 1996: Prey selection and prey removal by tiger (*Panthera tigris*) during the dry season in lowland Nepal. - Mammalia 60: 363-373.

Sun, B.G., Yu, X.C., Zhang, E.D., Sun, H.Y. & Guan, G.S. 1999: A survey of the Amur tigers and far eastern Leopards in Eastern Heilongjiang Province in 1999. - International Cooperation Research Report. Wildlife Research Institute of Heilongjiang Province, Harbin, China, pp. 9-13.

Sun, H. 2011: Monitoring techniques using a Big Plot sample method for ungulates and other species of mammals. - Forestry Science and Technology 6: 33-35. (In Chinese).

Sunquist, M.E. 1981: The social organization of tigers *Panthera tigris* in Royal Chitwan National Park, Nepal. - Smithsonian Contributions to Zoology 336: 1-98.

Tamang, K.M. 1979: Population characteristics of the tiger and its prey. - International Symposium on the Tiger, New Delhi, India, p. 23.

Tian, Y., Wu, J.G., Smith, A.T., Wang, T.M., Kou, X.J. & Ge, J.P. 2011: Population viability of the Siberian tiger in a changing landscape: going, going and gone? - Ecological Modelling 222: 3166-3180.

Treves, A., Plumptre, A.J., Hunter, L.T.B. & Ziwa, J. 2009: Identifying a potential lion *Panthera leo* stronghold in Queen Elizabeth National Park, Uganda, and Parc National des Virunga, Democratic Republic of Congo. - Oryx 43: 60-66.

Wang, S. 1998: China Red Data Book of Endangered Animals. - Science Press of China, Beijing, China, 417 pp.

Wang, S.W. 2010: Estimating population densities and biomass of ungulates in the temperate ecosystem of Bhutan. - Oryx 44: 376-382.

Wang, S.W. & Macdonald, D.W. 2009a: Feeding habits and niche partitioning in a predator guild composed of tigers, leopards and dholes in a temperate ecosystem in central Bhutan. - Journal of Zoology (London) 277: 275-283.

Wang, S.W. & Macdonald, D.W. 2009b: The use of camera traps for estimating tiger and leopard populations in the high altitude mountains of Bhutan. - Biological Conservation 142: 606-613.

Wei, Z., Jin, H.J., Zhang, J.M., Yu, S.P., Han, X.J., Ji, Y.J., He, R.X. & Chang, X.L. 2011: Prediction of permafrost changes in northeastern China under a changing climate. - Science China-Earth Sciences 54: 924-935. (In Chinese).

White, C.R. & Seymour, R.S. 2005: Allometric scaling of mammalian metabolism. - Journal of Experimental Biology 208: 1611-1619.

Wikramanayake, E., Dinerstein, E., Seidensticker, J.,

Downloaded From: https://complete.bioone.org/journals/Wildlife-Biology on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

Lumpkin, S., Pandav, B., Shrestha, M., Mishra, H., Ballou, J., Johnsingh, A., Chestin, I., Sunarto, S., Thinley, P., Thapa, K., Jiang, G., Elagupillay, S., Kafley, H., Pradhan, N., Jigme, K., Teak, S., Cutter, P., Aziz, M. & Than, U. 2011: A landscape-based conservation strategy to double the wild tiger population. - Conservation Letters 4: 219-227.

Yu, X.C., Sun, B.G., Sun, H.Y., Guan, G. & Zhou, X. 2000: The distribution and population number of Amur Tiger in Heilongjiang Province. - Chinese Wildlife 21: 14-16. (In Chinese).

Zhang, E.D., Wang, T.H., Miquelle, D.G. & Kang, A.L. 2005: Recovery of the wild Amur tiger population in China: progress and prospect. - China Forestry Publishing House, Beijing, China, 286 pp. (In Chinese with an English summary).

Zhou, S., Sun, H., Zhang, M., Lu, X., Yang, J. & Li, L. 2008: Regional distribution and population size fluctuation of wild Amur tiger (*Panthera tigris altaica*) in Heilongjiang Province. - Acta Theriologica Sinica 28: 165-173. (In Chinese).

Zhou, S.C. & Zhang, M.H. 2011: An integrated analysis into the causes of ungulate mortality in the Wanda Mountains (Heilongjiang Province, China) and an evaluation of habitat quality. - Biological Conservation 144: 2517-2523.

Zhou, S.C., Zhang, M.H., Sun, H.Y. & Yin, Y.X. 2011: Prey biomass of the Amur tiger (*Panthera tigris altaica*) in the eastern Wanda Mountains of Heilongjiang Province, China. - Acta Ecologica Sinica 31: 145-153. (In Chinese).

Downloaded From: https://complete.bioone.org/journals/Wildlife-Biology on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use