Research

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Human impact and climate cooling caused range contraction of large mammals in China over the past two millennia

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Many species have experienced dramatic declines over the past millennia due to the accelerated impact of human activity and climate change, but compelling evidence over such long-term time scales is rare. China has a unique system archiving historical records of important social, meteorological, agricultural and biological events over the last three millennia. We derived historical species occurrences (0–2000 AD) based on a comprehensive review of literature. To detect the driving forces of range contraction, we used correlation and multiple regression to quantify the linear association between species range indices and climate variables (five temperature series and three precipitation series), as well as a human population size series. We also used a machine learning technique, random forest, to quantify the nonlinear effects of the climate variables and human population size. The southward retreat of the Asian elephant *Elephas maximus* and the rhinoceroses (*Dicerorhinus sumatrensis*, *Rhinoceros unicornis*, *R. sondaicus*) was closely associated with climate cooling and intensified human impact (represented by high population size), and the westward retreat of the giant panda *Ailuropoda melanoleuca* was associated with intensified human impact. One temperature series and human population size showed interactive effect on range shift of the Asian elephant and the rhinoceroses; the effect of temperature was positive at low population size, but negative at high population size. Our results imply that a higher temperature caused the northward or eastward range shift of the Asian elephant, the rhinoceroses and the giant panda, and currently this trend is impeded by human activities. We also illustrate how human activity and climate act synergistically to cause range contraction.

Due to the accelerated impact of human activity and global climate change, many wildlife species have experienced range shifts or contraction over the past centuries (Chapin et al. 2000, Ceballos and Ehrlich 2002, Zhang 2013). Numerous species have been driven out of their central habitats because of intensive anthropogenic activities (Ceballos and Ehrlich 2002, Millar et al. 2012). Recent climate change has caused many species to move toward the poles or regions of higher elevation, even to the point of global extinction (Parmesan and Yohe 2003, Root et al. 2003).

Range shifts over geological time scales tend to be based on fossil records and/or phylogenetic analyses. Global climate change has been proposed to affect the range changes of many species. During the Quaternary, the general pattern was for glacially-induced equatorward range shift (Hensen et al. 2011) and postglacial poleward range shift (Parmesan et al. 2000). In the Holocene, however, the earth had a warmer global average temperature than the previous glacial periods, with substantial climatic variation (Ruddiman 2001). Agriculture appeared around 10 000 yr ago, and since that time human activities, such as the rapid development of agriculture, industry and population expansion, have become an important driving force in shaping biodiversity distribution on the earth (Channell and Lomolino 2000, Zhang et al. 2010). It is believed that most large mammals in China have undergone extensive range contractions over the past two thousand years (Wen 2009). Compared to studies at geological and centurial scales, quantitative studies on the effects of climate change and human impacts on species range shift at the millennium scale are still lacking because the knowledge of historical species distribution is often either fragmentary or absent (Bonebrake et al. 2010).

China has unique historical records of important social, meteorological, agricultural and biological events over the last three millennia (Ma et al. 1965, Zhang et al. 2009, 2010, Tian et al. 2011). Over the past millennia, rare and large animals were noted in historical records. By extending the studies by Wen and Wen (2006), Wen (2009) systematically compiled a compendium on the spatial distributions of several large mammals based on thousands of documents, such as official dynastic histories, gazetteers, local historical chronicles, and many other historical accounts. In this study, we demonstrate patterns of range decline and explore possible causal factors (i.e. temperature and human impact) of range shift or contraction by focusing on those large mammals for which the historical record in China is mostly complete and reliable over the past two millennia. These species include two large mammals, the Asian elephant *Elephas maximus* and the giant panda *Ailuropoda melanoleuca*, and one large mammal group, the rhinoceroses (*Dicerorhinus sumatrensis*, *Rhinoceros unicornis*, *R. sondaicus*). These animals had very broad ranges in central and south China but have experienced dramatic changes in abundance and range over the past two millennia (Fleischer et al. 2001, Louys et al. 2007). Wen and Wen (2006) and Wen (2009) proposed that temperature and human impact were two key factors affecting range shift of these species. However, quantitative analysis has not been conducted, and it is not clear how environmental factors and human activity interacted in affecting the range shift of these animals. In this study we quantity the independent and interactive effects of environmental factors and human activity on the range shift of these species in China during the past two millennia through the use of historical records.

Methods

Species range data

Both the Asian elephant and the giant panda include only one species in China and are easily distinguishable from other animal species due to their unique morphological properties. However, there are three species of rhinoceros in China: the two-horned Sumatran *Dicerorhinus sumatrensis*, the Indian rhinoceros *Rhinoceros unicornis*, and the one-horned Javan *Rhinoceros sondaicus*, and they were likely misidentified in the non-scientific literature published in early historical records (Wen 2009). The three rhinoceros species are sympatric animals, though they have different microhabitat demands. Given these constraints, however, we treat the three species as a rhinoceros group.

We obtained range information of the Asian elephant, the rhinoceroses and the giant panda from the compendium (Wen 2009) complied by R. Wen, based mostly on published and unpublished data collected by H. Wen. The latter authority was a famous historical geographer who collected and edited historical records on animals and plants during the 1940s. H. Wen identified occurrence sites of plants and animals by referring to standard histories and local gazetteers, as well as physical remains discovered in the recent decades. Standard histories, such as The Historical Records (~3000–122 BC), the Chronicles of the Han Dynasty (206 BC–23 AD), Twenty Four Histories (2550 BC–1644 AD), Zizhitongjian (403 BC–959 AD), and chronicles of other dynasties (up to the early 1900s), were frequently compiled and commented on by the central governments in the history of China (Wilkinson 2000). Local gazetteers (including provincial, prefectural, district, and county gazetteers) were compiled by local governments and include various types of information concerning historical, natural, economic, administrative, geographical and other aspects of a locality in China. The accounts of chance sightings, reports of human–animal conflict and captures constitute the principal sources of species occurrences. In the compendium, the use of historical literature records was conservative, records lacking other supporting observations were not included, and only confirmed records were adopted (Wen 2009).

Based on Wen's compendium (Wen 2009), we made a data table containing information about species name, year, and location of the target species. Most locations are recorded with county names. We digitized the maps of China in seven dynasties (Supplementary material Appendix 1, Fig. A1) based on Liang's book (Liang 1980), so as to determine the longitude and latitude of the centroids of ancient counties. The time-span and the number of records for these species are: the Asian elephant, 157 occurrences from 5000 BC to 2000 AD; the rhinoceroses, 1269 occurrences from 822 BC to 1997 AD; and the giant panda, 457 occurrences from 900 BC to 2004 AD. Because the occurrences recorded in far ancient time are very sparse, we only used the data of species occurrences in the last two millennia (0–2000 AD); total records for this time period were 146, 1053, and 423, respectively.

Some factors such as population density may influence the recording of animal occurrences, i.e. higher population density could cause higher recording intensity so as to have more records. We used Spearman correlation to check the association between the number of records in each county and population density in the county.

We established the decadal time series of the number of occurrences, latitude and longitude for each species. We calculated the mean latitude (Lat_{mean}), minimum latitude (Lat_{min}), maximum latitude (Lat_{max}), mean longitude (Lon_{mean}), minimum longitude (Lon_{min}) and maximum longitude (Lon_{max}) of the species occurrences to represent distribution center and ranges of the species at decadal scale. We also calculated these variables at 50-yr (Fig. 1) and 100-yr time scales to minimize potential impact of missing values or small sample sizes at the decadal scale.

Climate and human impact data

Temperature change and human population expansion (causing increased hunting and habitat destruction) have been suggested as the main factors affecting range shift of the Asian elephant, the rhinoceroses and the giant panda in ancient China (Wen and Wen 2006, Wen 2009). Over the past millennia, temperature has been shown to fluctuate in China, and human population expansion starting from the Yellow River regions of middle China in all directions, especially to northern and southern China. This would have greatly influenced the distribution range of the Asian elephant and the rhinoceroses inhabiting both tropical and subtropical regions, and the giant panda in the high elevation regions of south China. The impacts of precipitation and catastrophic climate events are unknown.

We employed five temperature series in our analyses. These included two temperature series representing temperature change of the globe (Mann et al. 2008), two representing

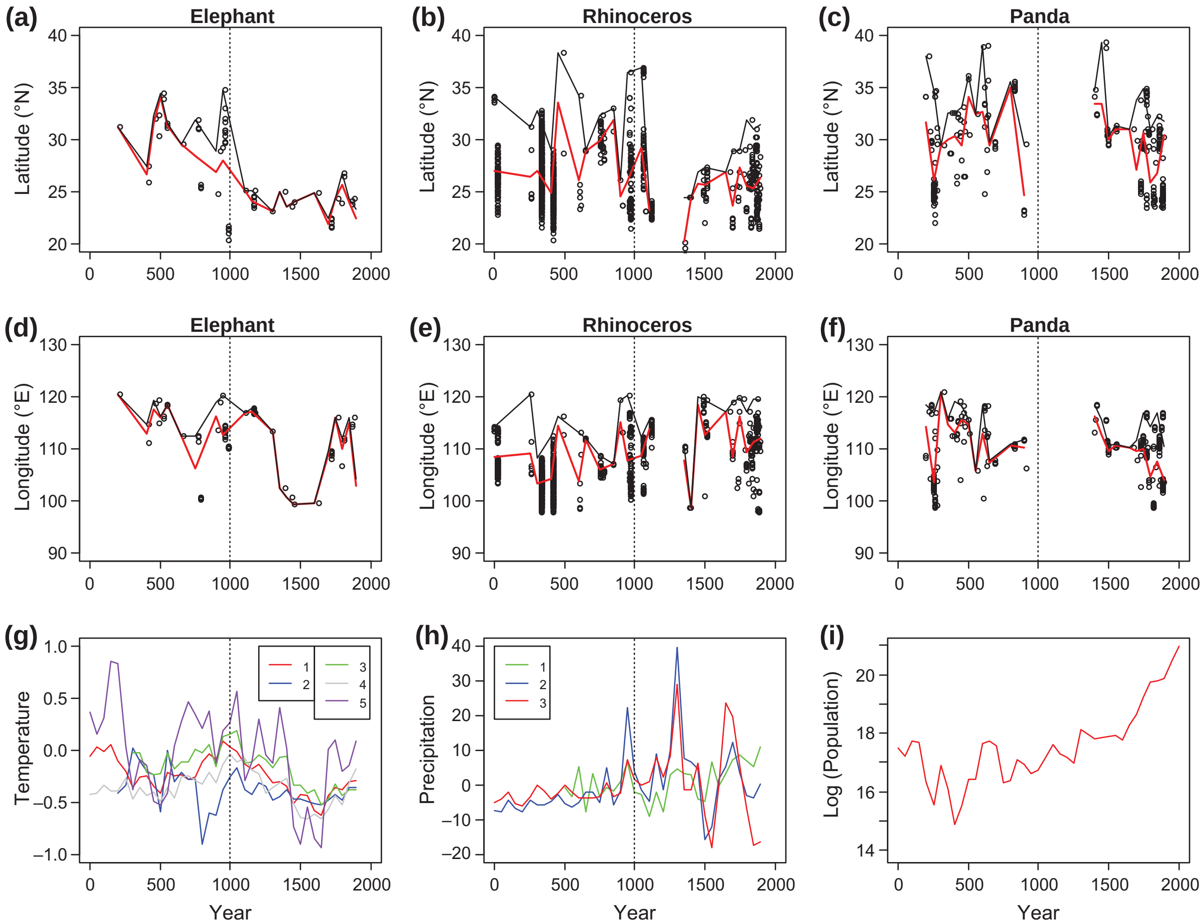

Figure 1. The historical northern and eastern limits of the ranges of Asian elephant, rhinoceroses, and giant panda in China, and time series for climate and population variables. Circles indicate the latitude (a, b, c) and longitude (d, e, f); red lines indicate the mean latitude or longitude at the 50-yr scale; black lines indicate the maximum latitude (northern boundary) or longitude (eastern boundary) at the 50-yr scale. The five time series of temperature are: 1. Temp.Ljungqvist, 2. Temp.Mann.cps.cru, 3. Temp.Mann.eiv.cru, 4. Temp.Moberg, 5. Temp.Yang. The three precipitation series are: 1. Precipitation, 2. Flood, 3. Drought. Human population sizes are natural logarithm transformed. Time series of temperature, precipitation and population size are shown in 50-yr time scale.

temperature change of the north hemisphere (Moberg et al. 2005, Ljungqvist 2010), and one representing temperature change of China (Yang et al. 2002) (Table 1, Fig. 1). These temperature series were the composite metrics based on various proxies at annual or decadal scales in certain parts of the past two millennia (Table 1).

We used three sources to represent precipitation change in China. One precipitation series is from Zheng et al. (2006), and one drought frequency series and one flood frequency series in China are from Zhang et al. (2009, 2010) (Table 1) based on Chen's summarization (1939). The drought/flood frequency data were obviously influenced by recording efforts in history (Tian et al. 2011). We corrected these two series by removing the effects of the total number of meteorological records (i.e. using the residuals of their linear regression). The total number of meteorological records were calculated by Tian et al. (2011) based on information in the compendium of Chinese meteorological records of the last 3000 yr, which was based on over 8000 pieces of recorded literature (Zhang 2004).

We established the time series of human population size based on Liang (1980) to represent the human impacts in China. Liang (1980) compiled historical documents and provided numerous tables listing the population sizes, household numbers, etc. in each administrative region in each year. We digitized the historical administrative boundaries and demonstrated the spatial distribution of population density in seven dynasties in China's history (Supplementary material Appendix 1, Fig. A1).

Statistics and models

We applied trend surface analysis (TSA) models to generate historical range shift patterns of the Asian elephant, the rhinoceroses, and the giant panda. The TSA model is a polynomial regression model using x-y coordinates of the occurrences as independent variables and the date (or year) of the occurrences as the dependent variable (Adjemian et al. 2007). We used the package spatial (ver. 7.3-3) in software R to generate the trend surface, based on regression of x-y coordinates with linear, quadratic, cubic, quartic and interaction terms.

We used Spearman correlations to check the simple linear relationships between the six indices of distribution

Table 1. Data sources of temperature series, precipitation series and human population size.

Variable	Region	Period (AD)	Original resolution	Seasonality	Data type	Reference
Temp.Yang	China (20°–42°N, 80°–130°E)	1–1999	Decadal	Annual	Composite of 9 proxies	Yang et al. 2002
Temp.Moberg	Northern Hemisphere (18°–90°N)	1–1979	Annual	Annual	Composite of 18 proxies	Moberg et al. 2005
Temp.Ljungvist	Northern Hemisphere (30°–90°N)	1–1999	Decadal	Annual	Composite of 30 proxies	Ljungqvist 2010
Temp.Mann.cps.cru	Global	200–1900	Annual	Annual	1209 proxy series	Mann et al. 2008
Temp.Mann.eiv.cru	Global	300–1900	Annual	Annual	1209 proxy series	Mann et al. 2008
Precipitation	Eastern China (105°–121°E, 25°–40°N)	501–2000	Decadal	Spring–autumn	Historical documents, mean of 48 stations	Zheng et al. 2006
Drought	Central, eastern, and southern China (97°–128°E, 18°–43°N)	0–1900	Decadal	Annual	Historical documents	Chen 1939
Flood	Central, eastern, and southern China (97°–128°E, 18°–43°N)	0–1900	Decadal	Annual	Historical documents	Chen 1939
Human population size	Central, eastern, and southern China (97°–128°E, 18°–43°N)	0–2000	Annual	/	Historical documents	Liang 1980
Number of meteorological record	Central, eastern, and southern China (97°–128°E, 18°–43°N)	0–2000	Annual	/	Historical documents	Zhang 2004

range (i.e. Lat_{mean}, Lat_{min}, Lat_{max}, Lon_{mean}, Lon_{min}, and Lon_{max}) and every temperature variable, precipitation variable, and the human population index. Then, we applied multiple linear regression to determine the partial and interactive effects of factors affecting range shift. Regression models were established as follows:

$$R_i = a + bT_i + c P_i + d H_i + e T_i \times P_i + f T_i \times H_i + g P_i \times H_i + \varepsilon$$

where a, b, c, d, e, f and g are constants, R_i is the index of distribution range at time *i*; T_i is the temperature; P_i is the precipitation; H_i is the human population size; ε is the normal distributed stochastic error. We selected only the variable with the largest and significant Spearman correlation coefficient into the regression model for each of the three kinds of variables (i.e. temperature, precipitation and human population size).

We further used a more complex model, random forest (RF) (Breiman 2001), to study the association between explanatory variables and species range indices, because RF is able to handle the nonlinear and interactive effects. RF also can evaluate the effects of all explanatory variables simultaneously, whereas multiple linear regression is affected by multicollinearity so that model selection must be carried out to remove insignificant variables. RF is an ensemble classifier that consists of many decision trees. It has higher performance than most other regression, classification, or machine learning models (Li and Wang 2013). We included all nine explanatory variables (i.e. nine series of temperature, precipitation and human population size) in the model to explain the species range indices, ranked the importance of the explanatory variables, and demonstrated the partial effects of these variables on species range indices.

Results

Range shift

Both latitude (Lat_{mean}, Lat_{max}) and longitude (Lon_{mean}, Lon_{max}) of the Asian elephant showed a decrease (southwestward retreat) from AD 0 to 1500, but they increased slightly after AD 1500 (especially for longitude) (Fig. 1a, d). Both latitude and longitude of the Asian elephant declined rapidly after AD 1900; presently, Asian elephants only occur in a small area in Yunnan Province, southwest China (Zhang and Wang 2003), near China's border with Burma (Myanmar) and Laos. Lat_{mean} of the rhinoceroses became smaller after AD 1000, indicating its southward retreat (Fig. 1b). There have been no sightings of rhinoceroses in China since 1950. Both Lat_{mean} and Lon_{mean} of the giant panda decreased after AD 1500, showing its southwest range contraction (Fig. 1c, f).

TSA provides more general patterns of the range shifts of these species. These analyses reveal that during the past two millennia ranges of both the Asian elephant and the rhinoceroses retreated southwestward (Fig. 2a, b), while the range of the giant panda retreated to the west (Fig. 2c).

Linear association between species range indices and environmental variables

We conducted correlation analyses for the six range indices and nine environmental variables using the time series dataset at three time scales (10-, 50- and 100-yr). Results were similar at all three temporal scales so we only present results for the 50-yr scale (Table 2); results for the 10- and 100-yr scales are provided in Supplementary material Appendix 1, Table A1 and A2, respectively. Latitudes of the Asian elephant and the rhinoceroses exhibited significant positive associations with some temperature series, while longitude was significantly negatively associated with a few temperature series for rhinoceroses. The association of range indices with precipitation variables (average precipitation, number of flood events, and number of drought events) was consistently negative (only except for: longitude of panda vs. drought). Human population size had a strong and consistent negative association with all range indices of the three species.

Multiple linear regression models with high R^2 values are listed in Table 3 (50-yr scale data). Compared with

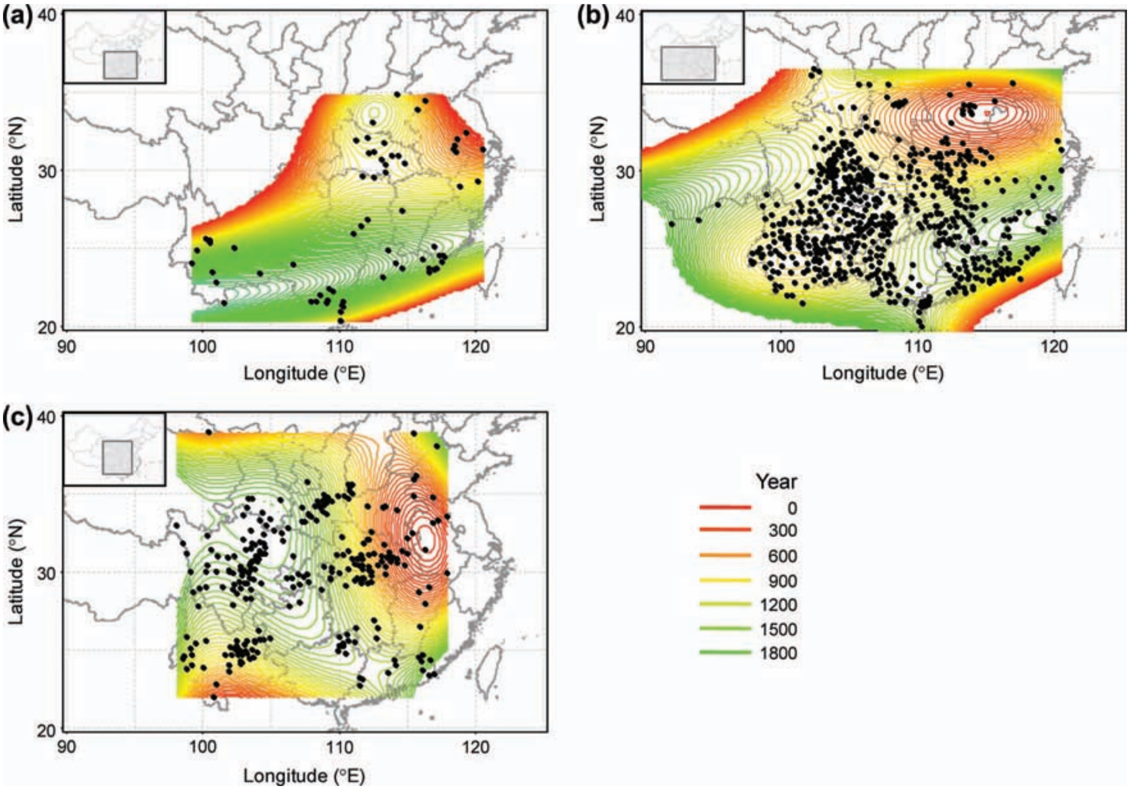

Figure 2. Patterns of range shift of Asian elephant (a), rhinoceroses (b), and giant panda (c) over the past 2000 yr by using trend surface analysis. The colored lines show the range shift pattern from red to green in time.

correlation analysis, multiple linear regression can represent the effects of many variables in one model. In this case, after model selection based on AIC, only a few terms are remained. Results from multiple linear regression (based on sign – positive or negative – of model coefficients) were consistent with those conducted using correlation analysis. Most of the interaction terms in the regression models are not significant. The only significant interaction term is Temp.Mann.eiv.cru × Population for the dependent variable Lat_{max} (for elephant and rhinoceros respectively). When human population size was low, latitude and temperature tended to have positive associations; whereas when human population size was high, these associations became negative (Supplementary material Appendix 1, Fig. A2).

Nonlinear associations between species range indices and environmental variables

Random forest demonstrates similar trends of the effects of environmental variables on species range indices, as those based on correlation and multiple regression analyses. Yet, RF provides more detailed response curves of the association (e.g. Supplementary material Appendix 1, Fig. A3).

Table 2. Spearman correlation coefficients for mean and maximum latitude/longitude of the northern/eastern distribution boundaries of the three species/groups with the five temperature series, three precipitation series and one population series (50-yr scale data). The coefficients in bold refer to significant coefficients.

	Asian elephant				Rhinoceroses				Giant panda			
	Lat_{mean}	Lon_{mean}	Lat_{max}	Lon_{max}	Lat_{mean}	Lon_{mean}	Lat_{max}	Lon_{max}	Lat_{mean}	Lon_{mean}	Lat_{max}	Lon_{max}
Temp.Yang	−0.06	−0.04	0.00	0.08	0.26	−0.43**	0.33	−0.31	0.00	−0.16	0.28	0.17
Temp.Ljungqvist	0.37*	**0.54****	0.47**	**0.68****	0.19	−0.30	0.41*	−0.16	−0.11	−0.12	0.06	0.14
Temp.Moberg	0.01	0.16	0.15	0.29	0.14	−0.16	0.18	−0.13	−0.13	−0.21	0.02	0.08
Temp.Mann.cps.cru	0.25	0.22	0.26	0.21	0.35	−0.39*	**0.46****	−0.28	−0.19	0.11	−0.12	0.34
Temp.Mann.eiv.cru	**0.43***	0.17	**0.49****	0.34	0.27	**−0.53****	0.30	**−0.56****	0.22	0.37	0.05	0.21
Precipitation	−0.49**	−0.16	**−0.43***	−0.10	−0.08	−0.13	0.27	0.38	−0.28	−0.17	0.07	0.28
Drought	−0.29	−0.04	−0.22	−0.03	−0.03	0.17	−0.23	0.03	0.30	0.31	0.32	0.00
Flood	**−0.67****	**−0.44***	**−0.54****	−0.35	−0.31	0.22	−0.31	0.27	0.01	−0.11	0.16	−0.10
Population	**−0.82****	**−0.55****	−0.67**	**−0.60****	−0.25	0.18	**−0.40***	0.11	−0.04	**−0.56****	−0.17	−0.49**

**Significance at the alpha level 0.05.
*Significance at the alpha level 0.1.

Table 3. Multiple linear models associating species range indices with temperature, precipitation and population using 50-yr scale data*.

Dependent variable	Model	R^2
Asian elephant		
Lat_{mean}	60.03 – 1.92 Population	0.568
Lat_{max}	104.53 + 191.01 Temp.Mann.eiv.cru – 4.41Population – 10.55 Temp.Mann.eiv.cru:Population	0.636
Lat_{max}	50.99 – 1.33 Population	0.301
Lon_{mean}	118.24 + 24.94 Temp.Ljungqvist	0.307
Lon_{max}	121.42 + 31.82 Temp.Ljungqvist	0.455
Lon_{max}	149.58 – 2.12 Population	0.222
Rhinoceroses		
Lat_{max}	118.7 + 302.06 Temp.Mann.eiv.cru – 5.11Population – 16.93 Temp.Mann.eiv.cru:Population	0.43
Lon_{mean}	109.45 – 5.62 Temp.Yang	0.224
Lon_{mean}	107.55 – 12.68 Temp.Mann.eiv.cru	0.248
Lon_{max}	111.65 – 15.6 Temp.Mann.eiv.cru	0.308
Giant panda		
Lon_{mean}	136.76 – 1.49 Population	0.289

*Only models with high R^2 values are listed.

The results of RF suggest that human population size was the most important variable that had negative association with all species range indices (except for maximum longitude of the giant panda). Two temperature series (Temp.Ljungqvist and Temp.Mann.eiv.cru) were ranked as the second and third important variables (Supplementary material Appendix 1, Table A3).

Discussion

During the past two millennia, the Asian elephant and the rhinoceroses experienced an extensive southward retreat, while the geographic range of the giant panda moved westward. Although the data on historical occurrences of these species are very sparse, we can still quantify that the expansion of the human population and fluctuations in temperature played important roles in the millennium-scale changes in the geographic ranges of these species.

Our results suggest that the Asian elephant and the rhinoceroses tended to move northward when temperature was high. These findings are consistent with many studies at geological and centurial scales (Fleischer et al. 2001, Louys et al. 2007, Louys 2012), indicating that temperature has had a similar effect on the range shifts of animals at different time scales. Our results are also consistent with the qualitative analysis by Wen and Wen (2006) that changes of northern boundaries of Asian elephant and the rhinoceroses might be associated with fluctuations of temperature. Both the Asian elephant and the rhinoceroses showed obvious southwestward contractions after AD 1000, and expansions since about AD 1500. These observations corresponded well with the change in temperature that showed a steady decline since AD 1000 (close to the Medieval Warm Period) (Fig. 1g), and became very low around AD 1500 (close to the period of the Little Ice Age). In contrast with the Asian elephant and the rhinoceroses, the giant panda's northern boundary showed no obvious retreat (Fig. 2c). It is notable that the Asian elephant and the rhinoceroses, as tropical and subtropical species, exhibited significant changes in their respective northern boundaries, but not their southern boundaries. Thus temperature appears to be a major driving force affecting their northern range shifts.

Under the accelerated pressure of recent global warming, many species have shifted their northern boundary toward the poles or to higher elevations (Parmesan and Yohe 2003, Root et al. 2003). Although temperature showed a rapid increase during the industrial period, all three of these charismatic mammals showed dramatic retreat of their northern/eastern boundaries since 1900 (Fig. 3). Such changes in their respective geographic ranges probably resulted from human impact, such as expanding agricultural practices, which was an overwhelming force that prevented these large animals from returning to their original habitats, as these habitats had been more or less altered. In short, a warming climate alone was insufficient to allow them to return to the north/east of China in modern time. Regression analysis indicated there was an interactive effect of temperature and human population size on the maximum latitude (the northern boundary) of the Asian elephant and the rhinoceroses. This result probably occurred because when human population size is low, warmer climate can trigger a northward range shift; however, when human population size is high, the effect of human population would override the effect of temperature.

Recent studies indicate that many species show contraction or range shift due to intensive anthropogenic activities (Ceballos and Ehrlich 2002, Li et al. 2009). Our results also indicate that, at a millennial scale, human population size showed significant effects on the range contraction of the species studied here. In the early1900s, China started its modern industrialization and, especially since 1949, the speed of industrialization has accelerated along with a rapid increase of population expansion, including extensive cultivation and urbanization, which is likely to have imposed significant negative effects on these large species. The Asian elephant and the giant panda have declined dramatically, and the rhinoceroses became extinct in China during the early 20th century (Sun et al. 1998).

Currently, there are approximately 200–250 Asian elephants (Wang 1998, Zhang and Wang 2003) and 2500–3000 giant pandas (Zhan et al. 2006) in the wild in China. From 1950 to 2004, natural forests in China declined to 30% of the total forest area (Li 2004). The sharp decline in the quantity and quality of natural forests has resulted in loss and fragmentation of natural habitats.

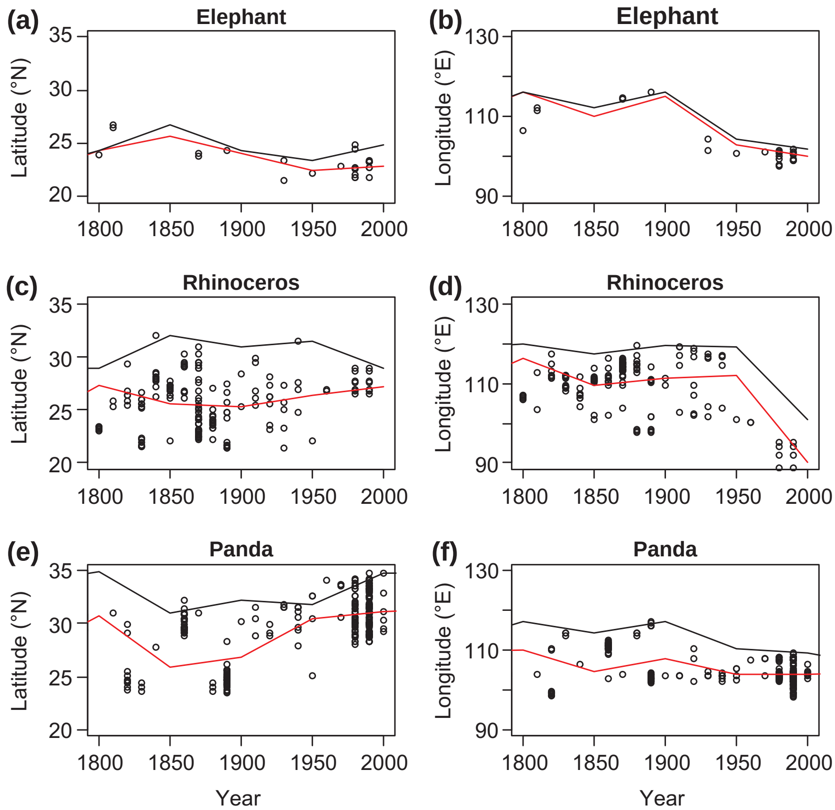

Figure 3. The historical northern and eastern occurrences of Asian elephant, rhinoceroses, and giant panda in China from 1800 to 2000. Circles indicate the latitude and longitude; red lines indicate the mean latitude or longitude at the 50-yr scale; black lines indicate the maximum latitude or longitude at the 50-yr scale.

However, after the implementation of the logging ban in 1998, forest resources have started to recover (Xu et al. 2009). Over the past 50 yr, the Chinese government established two reserves to protect the Asian elephant and 13 reserves to protect the giant panda. The effectiveness of these nature reserves is varied yet the rapid habitat loss has been stopped. Populations of the Asian elephants and the giant panda now are stable and are expected to increase in the future.

Asian elephant populations occurred in Java and Borneo, Indonesia since the Pleistocene (Louys et al. 2007, Cranbrook et al. 2008). A phylogeographic study suggests a contraction–expansion scenario during severe climatic oscillations during the Quaternary (Vidya et al. 2011). Another study suggests populations of Asian elephant reduced in size and became highly fragmented during the past 3000 to 4000 yr (Fleischer et al. 2001). Based on records in Chinese historical literature, Wen and Wen (2006), reported that the northernmost range of the Asian elephant reached Beijing (latitude 40°N) in 5000–900 BC when the climate was much warmer than the present, but from approximately AD 1830 to present, the Asian elephant has inhabited only small parts of Yunnan in China, and the population is fragmented throughout south Asia. The rapid southward range shift occurred around AD 1000; a time when temperature began to drop and the frequency of drought/flood disasters increased. Human population size did not show a significant increase during this period, suggesting that the range shift was likely caused primarily by climate change. Indeed, the Asian elephant showed obvious recovery in eastern China with increasing temperatures after the Little Ice Age (around AD 1500) until 1900, in spite of an increasing human population size. It is notable that frequency of floods showed negative effects on the latitude of the Asian elephant, suggesting that flooding may destroy habitat near rivers or in valleys.

Asian rhinoceroses consist of three living species, the greater one-horned rhino, the Javan rhino, and the Sumatran rhino, as well as more than a dozen fossil species in Asia (Antoine 2012). By the end of the Pleistocene, rhinoceroses disappeared from wide tracts of Asia, but remained in southeast Asia (Cerdeno 1998). There were three species of rhinoceroses in China. Their remains have been found in 78% of anthropogenic sites (Tong 2001). The range contraction of northern boundary of rhinoceroses in China is similar to that of the Asian elephant, likely because they are both large tropical and subtropical mammals. The northern range of the rhinoceroses reached the Yellow River region (latitude 40°N) around 1000 BC (Wen 2009). However, by AD 1450, the rhinoceroses appeared in only Yunnan and Guangxi, in the southwestern part of China. They became extinct in China in the early 20th century (Sun et al. 1998). Besides climate cooling, hunting was also an important factor in accelerating the range contraction of the species (Wen and Wen 2006). The latitude over which rhinoceros occurred also declined rapidly around AD 1000, but had an obvious increase since AD 1500. This supports our conclusion that its range shift was primarily caused by temperature change, and not by human activity. Since 1900, the geographic range of the rhinoceroses contracted rapidly toward the southwest until they finally became extinct in China. This extinction is almost certainly due to the impact of human activity.

Fossil *Ailuropoda* were widespread in south China and southeast Asia during the Pleistocene (Louys et al. 2007). The extant *A. melanoleuca* is a temperate species living in mountains with altitudes between 2000–4000 m (Hu and Schaller 1985). Tougard et al. (1996) examined its disappearance from southeast Asia, and attributed it to changes in bamboo distribution during the Pleistocene. They postulated that during the Pleistocene, temperate bamboo species were widespread in Thailand, therefore the *Ailuropoda* migrated southward. In the late Middle Pleistocene, climatic conditions became unfavorable for temperate bamboo in Thailand; so the temperate bamboo community subsequently retreated northwards, with *Ailuropoda* following its food until it reached its present range in southwest China (Nowak 1999). *Ailuropoda* occurred in Burma (Myanmar), Thailand and Laos until the Middle Pleistocene, and in Vietnam until the Late Pleistocene (Louys et al. 2007). In China, the northern range of the giant panda reached Beijing (latitude 40°N) in the Middle and Late Pleistocene, but over past five thousand years gradually shifted south and west (Wen and Wen 2006). The giant panda now occurs mainly in small parts of Sichuan, Shanxi, and Gansu (Qi et al. 2012). The giant panda eats mainly bamboo, so the disappearance of bamboo due to agricultural cultivation is believed to be the main factor underlying range contraction (Louys et al. 2007). Our results indicate that human activity has been more important than climate in affecting range contraction of the giant panda. In contrast with the Asian elephant and the rhinoceroses, the giant panda is a temperate species living at a high elevation. This may explain why no significant correlation between mean or maximum latitude or longitude of the giant pandas and temperature is found at the millennium scale. Altitude shift may be an alternative to movements along latitudes in responding changes of temperature. The large gap in occurrence data for the giant panda (Fig. 1c, f) underscores the need for further investigation on how climate effects range shift of this species.

It is notable that either global or northern hemisphere temperature (e.g. Temp.Ljungvist, Temp.Mann.eiv.cru) change had a higher performance in links with range shift of the Asian elephant and the rhinoceroses than did the temperature of China (i.e. Temp.Yang). Indeed, many studies indicate that global climate indices are often better than local climate indices in analyzing the relation of a species with the environment (Hallett et al. 2004). This is likely because the local climate often exhibit more high-frequency variation than those at regional or global scales and thus easily obscures its relation with biological indicators.

Historical data may be imbalanced in time and space due to variation of recording efforts of people (Bonebrake et al. 2010), and thus these records have some limitations (Skelly et al. 2003). However, they still have the potential to provide valuable insights into the long-term changes in species abundance, as well as occurrence (Kittinger et al. 2013). For species studied here, historical records are much more limited in the Xi Jin and Yuan dynasties those in other dynasties (Supplementary material Appendix 1, Table A4), indicating the unstable recording frequency over time (i.e. number of records per year in Supplementary material Appendix 1, Table A4). There is no linear trend of recording frequency in the past two millennia, although human population has gradually increased. The recording intensity should be positively associated with human density, yet the decreasing animal abundance neutralized increased recording intensity when human density was higher. We compared the spatial distribution of species occurrences with counties, and found that across six dynasties (with only two exceptions), the number of species occurrences is not related to population density or size and the area of the county where the animal were recorded (Supplementary material Appendix 1, Table A5). Thus, these data can be used for statistical analysis directly without further transformation. Our results provide evidence of climate change and human disturbance on range shifts by large mammals on a millennium scale by using historical records, thereby filling in gap of knowledge between geological and decadal-centurial scales.

Our results may have implications for the protection of these large mammals. As shown here, global warming enabled range expansion of the Asia elephant and the rhinoceroses, whereas human impact impeded these climate-driven range expansions, and, instead, caused range contraction. There is a need to increase natural habitats and strengthen protective measures for these charismatic mammals, especially along the northern boundary of the Asia elephant and the rhinoceroses, as well as in the high altitude regions of the giant panda, in order to assist these animals in expanding their ranges under the current and on-going period of global warming.

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Supplementary material (Appendix ECOG-00795 at <www.ecography.org/readers/appendix>). Appendix 1.