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# Predicting threat of climate change to the Chinese grouse on the Qinghai-Tibet plateau

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The Chinese grouse *Tetrastes sewerzowi* is restricted to small mountain areas on the southeastern edge of Qinghai—Tibet plateau. Recent evidence indicates that the global climate has undergone rapid change. To assess the potential effects of climate change on Chinese grouse, we applied a maximum-entropy modeling (MaxEnt) method to predict the current and future distributions of this species for three time periods: 2020, 2050 and 2080 in two greenhouse-gas emissions scenarios (A2a and B2a), which assume a medium and a lower increase in CO<sub>2</sub> emissions, respectively. Our modeling revealed that: 1) the size of suitable areas for grouse will decline over time, especially in emissions scenario A2a; 2) range shifts will happen at both latitudinal (northward shift) and elevational direction (upward). In addition, habitat expansion will be limited relative to loss, especially in the more distant future. Although the size of suitable area will not change greatly in the near future (e.g. 2020 and 2050), as predicted in the emissions scenario A2a in 2020, habitat will become more fragmented. Therefore, we suggest that the habitat fragmentation be considered with range shifts calculation while assessing the climate change threats. To cope with the ongoing climate change, either the protected area of the existing reserves should be expanded or new reserves should be established to accommodate range shifts. Reforestation and gouse population monitoring should also be conducted in the reserves to track response of grouse to climate change.

Recent evidence indicates that the global climate is undergoing rapid change, and is predicted to continue over the next century (Easterling et al. 1997, Leech and Crick 2007, IPCC 2007, Solomon et al. 2007). It has long been recognized that the contemporary climate is related to species distributions (Hawkins et al. 2003). Therefore, climate change may pose a threat to species by affecting population dynamics (Waite and Strickland 2006), distributions (Hughes 2000, Walther et al. 2002, Zimbres et al. 2012) and the spatial struture of the suitable habitats (i.e. fragmentation, Lu et al. 2012a, b). These threats could result in local population extinction (Thomas et al. 2004), especially for species having narrow thermal tolerance (Forero-Medina et al. 2011), such as the montane species (Pounds et al. 1999) and species living in northern latitudes, like polar bears Ursus maritimus (Hunter et al. 2010).

All grouse species only occur within the temperate, boreal and Arctic biogeographical zones of the northern hemisphere (Johnsgard 1983). They are adapted to cold climates, as indicated by feathered feet and nostrils and long intestines with well-developed caeca that enable them to digest coarse winter foods (e.g. buds and conifer needles; Johnsgard 1983). Because they are adapted to cold climates, it is hypothesized that they evolved in northern latitudes (del Hoyo et al. 1994). Among them, the Chinese grouse *Tetrastes sewerzowi* is a rare

species (Storch 2000, Sun et al. 2003) and has been listed as Near Threatened with decreasing trend by IUCN (IUCN 2012). It is endemic and restricted to conifer-dominated forests with deciduous trees on the southeastern edge of Qinghai—Tibet plateau (Sun et al. 2003). In many areas, only the wetter northern slopes have forest vegetation that support grouse populations (Sun et al. 2003), which results in fragmentation of its habitat. Furthermore, large-scale deforestation and intensive livestock grazing exacerbates habitat loss and fragmentation (BirdLife International 2001, Klaus et al. 2009). Therefore, we hypotheize that climate change threatens this species not only by influencing range shifts, but also by increasing habitat loss and fragmentation.

There are many species distribution modelling (SDM) methods to predict the potential distributions and estimate climate change effects through projection of future species distributions (Pearson and Dawson 2003, Guisan and Thuiller 2005, Elith et al. 2006, Elith and Leathwick 2009). By comparing predicted distributions under current conditions to future climate change scenarios, managers can develop more effective and suitable conservation plans (Araújo and Rahbek 2006). Therefore, we use the maximumentropy SDM method (Phillips et al. 2006) for scenarios relavent to 2020, 2050 and 2080 to predict the potential climate change threats to Chinese grouse as a way to enchance

conservation planning. Then we assess these threats from the perspectives of range shifts and changing spatial structure of suitable habitat. Climate change may entail habitat loss and upward shifts of habitat, which could exacerbate habitat fragmentation, and thus change the spatial structure (Lu et al. 2012a, b). Here we try to assess the habitat fragmentation aspect by comparing some specific landscape metrics.

#### Methods

We constructed SDMs for Chinese grouse *Tetrastes sewerzowi* within China. We used the same set of grouse location (observation) records as those used by Lu et al. (2012a). We reduced spatial autocorrelation (Dormann et al. 2007) by setting a spatial distance threshold of 0.083 decimal degrees (i.e. 5', about 8 km) between location records. The location record was included only if the spatial distances with all other location records was larger than the threshold. Using these filtering criteria, we had 41 location records, which we used to construct the SDMs.

#### **Environmental predictors**

To construct SDMs for the Chinese grouse, we collected 22 environmental predictors belonging to two different categories (bio-climatic and topographic, Supplementary material Appendix l Table A1). We obtained 19 bio-climatic predictors from the WorldClim database (Hijmans et al. 2005), which have been used to predict distributions of other species (Peterson et al. 2006, Cordellier and Pfenninger 2009, Lu et al. 2012a). We also used slope, aspect and compound topographic index, downloaded from the USGS database (<http://eros.usgs.gov>), as topographic predictors. For projecting future distributions, we extracted the same bioclimatic predictors for 2020, 2050 and 2080 from three internationally recognized general circulation models (GCMs) (CCCMA, CSIRO and HadCM3) with two IPCC greenhouse gas emissions scenarios (A2a and B2a) (IPCC 2001). According to IPCC Special Report on emissions scenarios, the emissions scenarios cover a wide range of assumptions about main driving forces of future emissions, from demographic to technological and economic developments (Nakicenovic and Swart 2000). As suggested by McKenney et al. (2007), we selected the A2a and B2a, which reflected two climate scenarios based on a conservative and an extreme emissions scenario in the future. The A2a scenario was projected for less environmentally conscious, and less regionalized solutions to economic, social, and environmental sustainability than the B2a scenario (Zhang and Liu 2005, Hu and Jiang 2011, Araújo et al. 2011). Therefore, the A2a scenario described a world with higher population growth rate, more rapid economic growth, faster land-use changes and unreduced emissions, while the B2a described a world with a reduced emission scenario where resource conservation would be promoted in the early decades of this century and the CO2 emissions would decline by midcentury (Nakicenovic and Swart 2000, Solomon et al. 2007). These data were available from the WorldClim database and the International Centre for Tropical Agriculture database (Hijmans et al. 2005, Ramirez and Jarvis 2008). We transformed all environmental predictors into a moderated resolution of 5' ( $\sim$ 8 × 8 km<sup>2</sup>) to construct the SDMs for the Chinese grouse.

#### SDM construction and evaluation

We modeled the distribution of Chinese grouse using MaxEnt (ver. 3.3.3k, Phillips et al. 2006). This model was a machine-learning algorithm for predicting the species potential distributions by combining the environmental predictors and the location data as input (Elith et al. 2011). MaxEnt used the location-only data and was appropriate for species with small samples of species locations (Elith et al. 2006, Pearson et al. 2007, Wisz et al. 2008). We selected the logistic output with suitability values ranging from 0 to 1, which represented the occurrence probability of target species (Phillips and Dudík 2008). Further parameter settings include: convergence threshold (10-5), regularization multiplier (1) and the maximum number of iterations (500). We used cross-validation with five replicates to assess the robustness of SDM (Fouquet et al. 2010, Lu et al. 2012b). The whole set of location records were partitioned as 80% training data and 20% testing data during each replicate. In order to decrease predictive uncertainty, we used the ensemble forecasting approach as suggested by Araújo and New (2007). We applied the basic mathematical function of mean ensembles to calculate the final logistic outputs (Marmion et al. 2009). Due to the uncertainties of different GCMs, we calculated the mean values of three projected suitability outputs (CCCMA, CSIRO and HadCM3) for the following analysis, which has become the most commonly used techniques and been shown to yield robust predictions (Hole et al. 2009, Marmion et al. 2009, Hu and Jiang 2011). During the modeling process, we selected the jackknife analyses of the regularized gain with training data to examine the importance of different predictors.

In order to evaluate the predictive performances of the SDMs, we selected the area under the receiver operating characteristic curve (AUC; Fielding and Bell 1997) to evaluate the predictions using the training and test data firstly. This measurement has been used extensively in the species distribution modelling literature (Loiselle et al. 2010), and has been considered the best practice for assessing SDM accuracy (Pearce and Ferrier 2000, Thuiller 2003, Rushton et al. 2004, Austin 2007). AUC values ranged from 0 to 1, where a value of 1 indicated perfect (100%) discrimination and a score of 0.5 indicated a model with discrimination that is no better than random (Pearce and Ferrier 2000). To test the reliability of the accuracy assessment, we also calculated Cohen's kappa statistic (kappa; Cohen 1960) and true skills statistics (TSS; Allouche et al. 2006) as suggested by Mouton et al. (2010). Both kappa and TSS values ranged from -1 to +1 where +1 indicated a perfect performance, while values < 0 indicated a performance no different to random (Cohen 1960, Allouche et al. 2006). We generated random pseudo-absences using the Random Points function of the R package dismo (Elith et al. 2006, Hijmans et al. 2010) and then using the presence.absence.accuracy function of the R package PresenceAbsence to calculate the kappa and TSS values (Freeman and Moisen 2008a).

#### Climate change threats assessments

For comparing distributions at future times, we projected species distribution for 2020, 2050 and 2080, respectively. To explore the climate change threats to the Chinese grouse, we calculated the range, position (i.e. range centroid) and elevation differences. Generally, range shifts predicted to occur from climate change may have three forms - shifting by latitude, by longitude and by elevation (Forero-Medina et al. 2011). The suitable area (i.e. the entire spatial area over which a species might be found) should be identified with a reasonable suitability threshold. We used the optimal.thresholds function in the PresenceAbsence R package (Freeman and Moisen 2008a) to calculate the suitable threshold and selected Pred Prev = Obs as the threshold following Freeman and Moisen (2008b) and Lu et al. (2012a). Subsequently, we extracted the altitude, longitude and latitude of each grid throughout the suitable area and compared these values between current and future distributions. Furthermore, we compared the habitat fragmentation between current and predicted future climate change scenarios. Specifically, we applied a square lattice to identify the continuous suitable patches for which we considered the target grid to be connected with eight neighboring grids (Lu et al. 2012a). After identifying the continuous patches predicted as suitable for Chinese grouse, we applied several landscape metrics to assess habitat fragmentation quantitatively (McGarigal and Marks 1995): suitable area size (SAS) by calculating the predicted suitable grid number; area size of concave polygon (ASP) which contains all suitable grids; proportion of suitable areas (PSA); number of patches (NP), patch density (PD, number of patches per 1000 km<sup>2</sup>), mean patch size (MPS), patch size standard deviation (PSSD) and patch size coefficient of variation (PSCV). All these calculations and classifications for the present and future distributions were performed using the program ArcGIS ver. 9.3.1 (Environmental Systems Research Institute 2009).

#### Results

#### **Modeling evaluation**

The kappa and TSS values of all SDMs were larger than 0.6, while the AUC values were larger than 0.9 (Table 1), which revealed that the SDMs performed well for the Chinese grouse. Cross-validation also suggested that the models were quite robust, because of the relatively high values of accuracy measurements for both training data and test data (Table 1). According to the jackknife test of variable importance, the mean temperature of driest quarter (BIO10), max

temperature of warmest month (BIO5), mean temperature of wettest quarter (BIO8), slope, temperature seasonality (BIO4) and isothermality (BIO3) achieved the highest gains when used in isolation, and thus appeared to have the most useful niche requirement information for the Chinese grouse.

## Area size and range shifts

Based on the current suitability map of Chinese grouse (Fig. 1), the distribution range was largely concentrated at the southeastern edge of Qinghai-Tibet plateau. The moutainous regions in southern Gansu, middle Sichuan and eastern Tibet were predicted to be relatively more suitable for this species (i.e. with redder color; Fig. 1). SDM predicted that the suitable area size will decline over time, especially in the A2a missions scenario (Fig. 2a). Although the suitable area size changed moderately for 2020 (+ 12.7% in A2a and -9.5% in B2a) and 2050 (-13.9% in A2a and -1.3% in B2a), there was a larger change of -55.9% and -23.4% for 2080 in A2a and B2a, respectively. Furthermore, the suitability was predicted to decline for all climate change scenarios (i.e. the mean suitability will decline from 0.643 to 0.632, 0.620 and 0.586 for 2020, 2050 and 2080 in emissions scenario A2a, and to 0.628, 0.624 and 0.608 in B2a, respectively; see also Fig. 2b).

Habitat loss and gain in different climate change scenarios during our timeframes indicated that horizontal range shifts should occur. Suitable areas on the southern, western and eastern margins of its current distribution would be lost, while newly gained suitable areas would be located mainly on the northern margin, especially in the more distant future, (e.g. 2080, Fig. 3). In addtion, some newly gained suitable areas in Tibet and western Sichuan in the near future (e.g. 2020 or 2050) would be lost in the more distant future (e.g. 2080; Fig. 3). According to the mean longitudes and latitudes of suitable areas, we found that climate change would require this species to shift northward generally (Fig. 4a). Furthermore, although patterns of habitat loss and gain were similar in different emissions scenarios, the magnitude of range change varied. In emissions scenario A2a, both the stable and newly gained areas showed declining trends, while areas lost areas should increase in the future (Fig. 4b). We found that 82.2% of current suitable areas should be stable in 2020, while this proportion should drop to 63.1% and 30.6% in 2050 and 2080, respectively. Newly gained areas were also predicted to decline from 30.5% in 2020 to 23.0% and 13.5% in 2050 and 2080, respectively. Range change will be less dramatic in emmisssion scenario of B2a (Fig. 4b). The stable areas will decrease from 73.2% in 2020 to 69.1% and 53.2% in 2050 and 2080, respectively. The

Table 1. Accuracy measurements of predictive SDMs for Chinese grouse. AUC = area under relative operating characteristic curves; TSS = true skill statistic; Kappa = Cohen's kappa statistic; Rep.1–5 represent the five replicates for cross-validation.

Accuracy		Rep.1		Rep. 2		Rep. 3		Rep. 4		Rep. 5	
measurements	Ensemble*	Training	Test								
TSS	0.893	0.941	0.933	0.894	0.800	0.921	0.762	0.914	0.838	0.906	0.864
Карра	0.717	0.833	0.718	0.730	0.705	0.773	0.629	0.790	0.805	0.824	0.823
AUC	0.976	0.989	0.972	0.972	0.930	0.984	0.920	0.980	0.972	0.983	0.913

<sup>\*</sup>Ensemble represents the result of averaged five replicates.

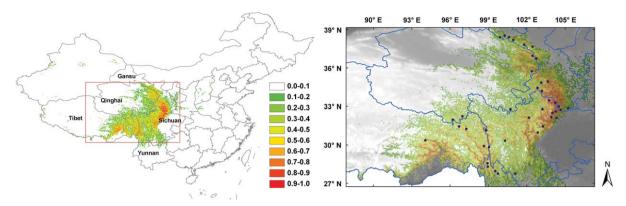


Figure 1. Mean predicted probability of occurrence (suitability) of the Sichuan jay under current situation, showing provinces in China. The color represents the suitability, from low (green) to high (red). The right figure shows the area marked by red square in the left one, and overlays with altitude (the whiter color indicates higher altitude). The dark blue dots are the occurrence records used for model calibration.

newly gained areas even showed an increasing trend from 17.3% in 2020 to 29.5% and 23.3% in 2050 and 2080, respectively. Finally, from the perspective of vertical (i.e. elevational) range shifts, the modelling results showed upward shifting under climate change (Fig. 4c). The mean altitude was predicted to increase from 3476 m to 3683 m, 3710 m and 3848 m in 2020, 2050 and 2080, respectively, in emissions scenario A2a, and from 3476 m to 3577 m, 3725 m and 3741 m in 2020, 2050 and 2080, respectively, in emissions scenario of B2a.

## **Habitat fragmentation**

In general, climate change was predicted to affect grouse through change in spatial structure of suitable areas. The mean patch size will be reduced, while the patch density will increase in both emissions scenarios and different time-frames (Table 2). Moreover, we found that although the value of patch size coefficient of variation would not change greatly in the near future (e.g. 2020 and 2050) and would even increase from 7.61 to 8.10 in 2020 in A2a, the modelling showed declining trends in both emissions scenarios.

According to the patch isolation maps (Fig. 5), both habitat loss and upward shift exacerbated the fragmentation, especially in the A2a scenario. In the middle of Sichuan Province (Fig. 5d–f), climate change would mainly compel Chinese grouse to shift upward. A large number of suitable grids at relatively lower altitudes would be lost, while newly gained suitable grids would be at even higher altitudes. Suitable habitat would become more isolated and perforated in the future (Fig. 5d–f). The patch isolation patterns of the other-timeframes can be found in the Supplementary material Appendix 1 Fig. A1.

## **Discussion**

#### Climate change threats

As the world's largest geomorphology unit, the Qinghai—Tibet plateau influences atmospheric circulation and affects the climate of eastern Asia (Sun 1996). Coniferous forest only occur in the mountainous areas at relatively higher altitude on the southeastern edge of the Qinghai—Tibet plateau.

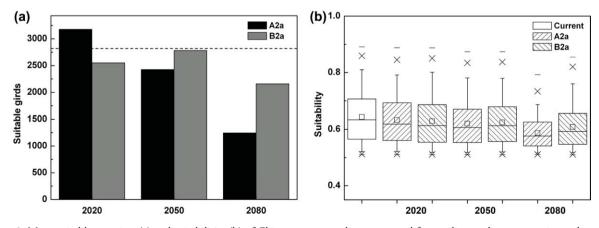


Figure 2. Mean suitable area sizes (a) and suitabilities (b) of Chinese grouse under current and future climate change scenarios at three time slices of 2020, 2050 and 2080 projected for the Qinghai–Tibet plateau. We use the number of suitable grids  $(8 \times 8 \text{ km}^2 \text{ resolution})$  to represent the size of suitable area. Current suitable grid number is illustrated using the dashed line in (a). The solid horizontal line represents the median, short horizontal lines represent the maximum and minimum, the square symbol represents the mean, edges of box are quartiles, whiskers are 5th and 95th percentiles and crosses are 1st and 99th percentiles.

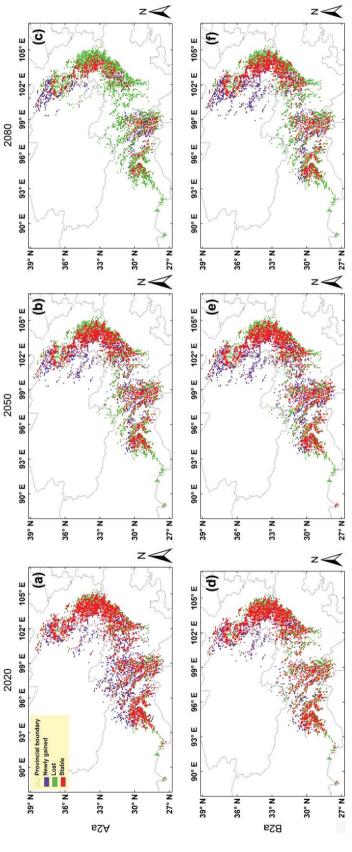


Figure 3. Predicted potential Chinese grouse habitat that is stable, lost or gained under climate change, based on two IPCC greenhouse gas emission scenarios of A2a (a, b, c) and B2a (d, e, f) and three time timeframes of 2020 (a, d), 2050 (b, e) and 2080 (c, f).

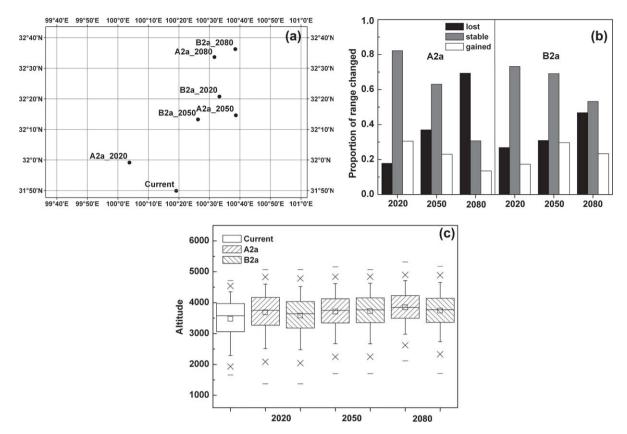


Figure 4. Climate change threats to Chinese grouse through range shifts. (a) the centroid of current and future suitable girds (through calculating the mean longitude and latitude values); (b) the proportion of habitat that is stable, lost or gained when climate change; (c) the mean altitude in current and climate change scenarios. The solid horizontal line represents the median, short horizontal lines represent the maximum and minimum, the square symbol represents the mean, edges of box are quartiles, whiskers are 5th and 95th percentiles and crosses are 1st and 99th percentiles.

These forests formerly belong to the more widely distributed Taiga forest, which has retracted to its present distributions during the uplifting of the plateau (Cheng 1981). Due to the unique natural ecological environment and geological history, many endemic species have evolved and live in these mountainous areas, such as the Sichuan jay *Perisoreus internigrans* (Jing et al. 2009, Lu et al. 2012b), blood pheasant *Ithaginis cruentus* (Jia et al. 2010), and snowy-cheeked laughingthrush *Garrulax sukatschewi* (Wang et al. 2011). Many of them have evolved specific survival strategies for local climates, which could hinder adaptations necessary during a regime of rapid climate change (Lu et al. 2012b).

Similar to other montane species (Sekercioglu et al. 2007, Wilson et al. 2007), our modelling revealed that

climate change may pose threats to Chinese grouse, and these threats would likely intensify over time. Thomas and Lennon (1999) proposed that the northern margins of British birds has already extended by an average of 18.9 km over a period of 20 years. Other studies have proposed that the species on montane zones could shift to the higher elevations (Pounds et al. 1999, Crick 2004). We found that the Chinese grouse distributions would shift northward and upward obviously under climate change scenarios (Fig. 3, 4). However, unlike species that have wide distributions or greater dispersal capabilities, the availability of suitablily predicted to expand under climate change would be limited for Chinese grouse because of their lesser dispersal capability. Moverover, it appeared that expansion of suitable habitat

Table 2. Quantitative habitat fragmentation assessment of the suitable areas for Chinese grouse. SAS = suitable area size (km²); ASP = area size of concave polygon (km²); ASP = area size of c

Scenarios		SAS*	ASP	PSA	NP	PD	MPS	PSSD	PSCV
Current		235060	821589	0.29	214	0.260	13.17	100.31	7.61
A2a	2020	264995	851896	0.31	274	0.322	11.60	87.14	7.51
	2050	202374	765673	0.26	240	0.313	10.11	74.36	7.35
	2080	103730	553421	0.19	197	0.356	6.31	25.91	4.10
B2a	2020	212713	827297	0.26	300	0.363	8.50	68.86	8.10
	2050	231975	792484	0.29	248	0.313	11.22	81.87	7.30
	2080	179943	714559	0.25	227	0.318	9.51	63.85	6.72

<sup>\*</sup> SAS is derived from the original calculated suitable grid number (multiplying 64 (the area of a grid) by grid number).

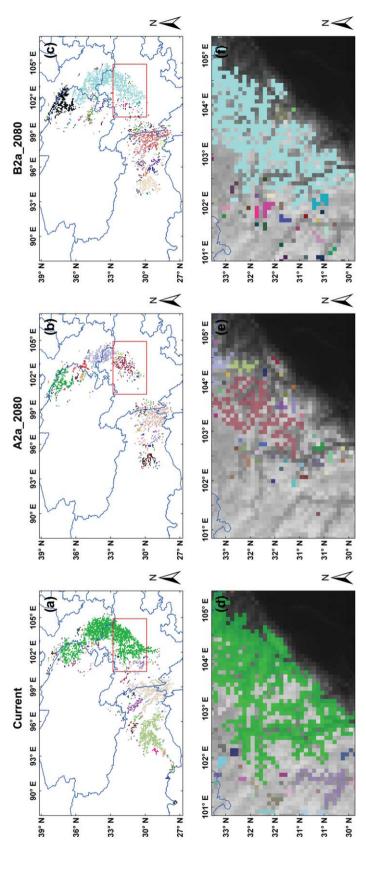


Figure 5. The isolation patterns of predicted suitable habitat for Chinese grouse. The isolated patches are indicated with different colors: (d), (e) and (f) shows the area marked by red square in (a), (b) and (c), respectively. The figures of (d), (e) and (f) overlays with altitude (the wighter color indicates higher altitude).

areas would not compensate for the loss of current suitable areas, especially under our distant future scenario (Fig. 4b).

Habitat fragmentation has long been recognized as one of the major causes of global biodiversity loss and local extinction (Kruess and Tscharntke 1994). Because of the high demands for farmland, timber and firewood by local people, deforestation of Chinese grouse's mountain habitats continued until 1998 when disastrous flooding happened there, which motivated greater conservation of forests (Sun et al. 2003). According to our modelling, climate change may exacerbate existing habitat fragmentation patterns (Table 2). This fragmentation may reduce or halt gene flow or perhaps increase the extinction risk of isolated populations (Lu et al. 2012b). Specifically, we found that fragmentation would happen in both patch isolation and within patch fragmentation (Lu et al. 2012a). The suitable area size would not change much in the near future (e.g. 2020 and 2050) and was even predicted to increase in emissions scenario A2a in 2020 (Fig. 2a). However, modelling predicted that habitat would become more fragmented rapidly such that the patch density would be increased in all climate change scenarios and timeframes (Table 2). Furthremore, although the values of patch size coefficient of variation were relatively stable in the near future, they showed accelerated declining trends (Table 2). Patch size coefficient of variation provided an index of patch to patch size variation relative to the mean value (McGarigal and Marks 1995, Jacquemyn et al. 2002). Therefore, the declining values of patch size coefficient of variation partially revealed that some currently connected large patches would become isolated and then reduce the size variability among patches. This conclusion was also observed in patch isolation (Fig. 5) where the orignal big suitable patch shown in green color (Fig. 5d) would be isolated into more small patches (Fig. 5e-f). We also found that the patches would show more internal fragmention. For example, the contour of big patch with green color in Fig. 5d did not change much in the B2a scenario, but the suitable habitat would become more perforated (Fig. 5f), and thus could decrease both the proportion of suitable areas and mean patch size. According to the quantitative habitat fragmentation assessment, the mean patch size would be reduced under all climate change scenarios and timeframes (Table 2). The proportion of suitable areas would change moderately in 2020 and 2050 but would decrease in 2080 in both scenarios (Table 2). It also showed a declining trend in the A2a scenario (Table 2). Finally, our modelling results validated the importance of a combinating habitat fragmentation analysis with range shift calculations when assessing the climate change threats using the SDM method.

## **Conservation implications**

Most grouse species are habitat specialists with fairly narrow habitat preferences, and thus are susceptible to habitat changes (Storch 2000). The Chinese grouse is one of the three grouse species listed as Near Threatened by IUCN. Our modelling suggests that although the climate change would not have immediate threats in the near future, the potential for negative effects would increase over time. Therefore, conservation managers should consider the effects of climate change when developing conservation

plans. First, the protected area of the existing reserve for Chinese grouse should be expanded or new reserves established according to the current distributions and potential for future range shifts. For example, only 23% mature forest in the Lianhuashan Mountains was within the Lianhuashan Nature Reserve (Sun et al. 2003). Therefore, more surrounding forest area should be included within the reserve. Chinese grouse have poor long-distance flying ability, thus, the major portion of travel time during dispersal will be spent walking, which is similar as ruffed grouse Bonasa umbellus (Godfrey and Marshall 1969). More and larger reserves could also improve the conservation efficiency through unified planning, such as establishing movement corridors among populations to facilitate dispersal maong habitat fragments. Furthermore, human activities such as illegal hunting and egg collecting still happens in local areas (Storch 2000). Egg collecting is apparently substantial (Sun et al. 2003). Lu and Sun (2011) even suggested that these activities may be the most important factors that influence the local population viability in Lianhuashan. Establishing or expanding reserves could also improve the individual survival rate through animal protection (e.g. protecting individuals from illegal hunting and restrict human activity during the breeding season) and community education about biodiversity conservation. Second, reforestation should be conducted throughout the mountain habitats of Chinese grouse, since rapid deforestation over the past century was largely due to humans rather than the natural factors. Finally, grouse population monitoring should be conducted, which would necessary to observe population trends and assess the success of the conservation efforts (Storch 2000). Furthermore, attention should be given not only to populations within the most suitable and continuous area, but also to populations at the northern and southern margins of the species' distribution (Lu et al. 2012b) because populations at the margins of distributions should be the most sensitive to the climate change.

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Supplementary material (available online as Appendix wb-13-024 at www. <www.wildlifebiology.org/readers/appendix>.). Appendix 1.

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