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Post-breeding habitat association and occurrence of the Snow Partridge (*Lerwa lerwa*) on the Qinghai-Tibetan Plateau, west central China

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Abstract

Background: Habitat selection is linked to a range of behavioral and non-habitat-related phenomena. The Snow Partridge (*Lerwa lerwa*) is a little known bird distributed along the Himalayas at high elevations in extreme habitat and a harsh climate. Unravelling the use of its habitat is important not only for understanding the ecology of this bird but also for its protection and conservation. Recent advances in modeling algorithms, in conjunction with the availability of environmental data, have made species distribution models (SDMs) widely accessible and used to predict available habitat and potential distributions.

Methods: We conducted a field study at Balangshan mountains on the Qinghai-Tibetan Plateau in west central China in August 2013. A line transect method and playback of recordings were used to survey suitable habitats. We established 20 m × 20 m plots at each flock location as well as control plots and measured 18 environmental variables. We used models of random forests to determine the micro-habitat variables that Snow Partridges might select, based on 25 presence and 27 absence locations and a maximum entropy algorithm (MaxEnt ver. 3.3.3.e) to predict their distribution in three counties, i.e., Wenchuan, Xiaojin and Baoxing in Sichuan Province, with a total area of 12,800 km², adjacent to our main study site.

Results: We found a total of 13 flocks of the Snow Partridge in our study area on pyramidal peaks, arêtes and steep rock slopes above 4430 m. The species is associated with habitats at the top of high cliffs or flatter terrain close to high cliffs, on more gentle slopes but still at high elevations. Terrain factors were the main factors affecting the selection of the micro-habitat by this partridge while vegetation is a more important factor at the meso-scale, with elevation as an important factor at both scales. Only 6.64% of our study area had features that might provide a suitable habitat for the Snow Partridge.

Conclusions: Movements of the Snow Partridge, covering elevations from 4400 to 4700 m, were significantly associated with their habitat selection, whether on a micro- or a meso-scale of the three counties. Scale effect is an obvious topographic factor affecting the birds to avoid predators at the micro-habitat level and vegetation structure at the meso-habitat level for accessing food. Post-breeding habitat selection seems a trade-off between food availability and predator avoidance.

Keywords: Lerwa lerwa, Habitat selection, Random forests, MaxEnt, Scale

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Background

Habitat selection carries with it a connotation of understanding complex behavior and life history, together with many non-habitat-related phenomena such as predation, food limitation and so on that can influence habitat selection in birds (Jones 2001). Due to vegetation and landscape heterogeneity, sometimes exhibiting hierarchical features, habitat selection is found to be scale-dependent (Kotliar and Wiens 1990; Orians and Wittenberger 1991; Jones 2001), especially when the different scales are observer-defined rather than organism-defined. Based on the biological characteristics of organisms, it is not sufficient to reflect the actual situation only at one scale (Kotliar and Wiens 1990). Scale is reflected in research on macro-ecology and global change that is relevant at global scale (Phillips et al. 2006; Elith and Leathwick 2009), whereas studies targeting detailed ecology, conservation planning and wildlife management may be most relevant at local or regional scale (Fleishman et al. 2001; Ferrier et al. 2002). Species-habitat analysis obliges ecologists to adopt multi-scale perspectives.

The study of habitat selection in birds has a long tradition. In the past two decades, empirical models have emerged that use species distribution data (presence or absence, or abundance at known locations) and environmental variables to evaluate species' ecological niche and predict species distribution across spatial and temporal dimensions. The trend has been driven by rapid development of geographic information system (GIS) and statistical science, and the innovation of species distribution models (SDMs) (Araújo and Guisan 2006; Araújo and Peterson 2012). SDMs have been applied widely in habitat selection studies and have increasingly become an important tool to address various issues in species conservation plan and wildlife management (Guisan and Thuiller 2005; Elith and Leathwick 2009; Guisan et al. 2013). The identification of priority areas for biodiversity conservation has become one of the leading topics for biodiversity conservation. In the Greater Himalayas, an internationally recognized biodiversity hotspot, Dunn (2015) and Dunn et al. (2016) showed pervasive declines of Galliformes, identified areas of high species richness and weighted distribution maps for each species based on models that incorporated specific conservation values. The approach facilitates proposals for optimizing the protected areas system (Dunn et al. 2016). However, the current conservation focus has meant that attention is biased towards threatened species and protected areas, as well as suffering from bias in the sources and ages of distribution data and bias towards more readily accessible sites (Boakes et al. 2010). Furthermore, the ways in which protected areas might be managed would require more detailed, local scale information on how multiple aspects of the habitat are used by any given bird (or other animal) species. For example, habitat fragmentation must be considered in conjunction with ecological requirements (Lu et al. 2012a).

The Snow Partridge (*Lerwa lerwa*), a little known bird of the family Phasianidae (Galliformes), is found along the Himalayas from eastern Afghanistan, Kashmir and eastern Pakistan, through mountainous north of India, Nepal, Bhutan, northern Myanmar and southwest China (Cheng et al. 1978; Li and Lu 1992; Zheng et al. 2002; Khanal et al. 2012). In China, the Snow Partridge is found in southern Tibet, northwestern Yunnan, western Sichuan and in the southwest of Gansu Province (Cheng et al. 1978; Zhao 2001), inhabiting a zone between the tree line and snow line at elevations between 3000 and 5200 m (Cheng et al. 1978; Del Hoyo et al. 1994; Xiao et al. 2014). The name 'Snow Partridge' is occasionally applied to members of the genus *Tetraogallus*, for example by Abbott and Christensen (1971).

Difficulty in conducting field work at high elevations and a rocky terrain is probably one of the reasons that only three publications are available for this species (Li and Lu 1992; Potapov 2000; Srivastava and Dutta 2010). Although considered 'fairly common' (Sathyakumar and Sivakumar 2007), 'not globally threatened' (Del Hoyo et al. 1994) and of 'Least Concern' (IUCN 2015), the Snow Partridge was reported to be suffering from severe threats due to hunting, habitat fragmentation as a common consequence of human development and disturbance from tourism and traffic (Srivastava and Dutta 2010). As well, its occurrence on steep rocky or grassy slopes with alpine scrubs, meadows, dwarf juniper and rhododendron bushes at very high elevations, where biodiversity is severely restricted (Sathyakumar and Sivakumar 2007), implies that it is close to the limit of ecological tolerance, i.e., conditions making this species highly vulnerable to climate change (Crawford 2008). Under these circumstances, the habitat could hardly be restored should it be damaged or destroyed (Niu et al. 2003; Crawford 2008).

Global warming has been responsible for partial melting of glaciers on the Qinghai-Tibetan Plateau (Liu et al. 2011). Since the 1980s, the thickness and extent of many glaciers have been reduced (Su et al. 1999; Liu et al. 2005, 2011) and the retreat of glaciers to higher elevations is expected to continue for the foreseeable future (Su et al. 1999). These trends are more serious at the edge of the Qinghai-Tibetan Plateau than those on the Plateau itself (Su et al. 1999; Pu et al. 2004). Since the Snow Partridge lives at elevations close to glaciers and the snow line, its habitat and therefore, its survival is likely to be affected.

However, we know little about the species-habitat relationships of the Snow Partridge which is a prerequisite for conservation efforts (Kotliar and Wiens 1990; Jones 2001; Schäublin and Bollmann 2011). Only qualitative descriptions of the distribution and habitat of this partridge have been available in the past (Lu 1988; Lu et al. 1989; Li and Lu 1992), usually embedded within broader studies of avian communities of which the Snow Partridge is a member (Li 1986; Lu et al. 1989; Li et al. 2010; Srivastava and Dutta 2010; Xiao et al. 2014).

Consequently, multi-scale research on habitat selection of this partridge is needed, not only for understanding its life history but, as well, for effective conservation management. The objectives of our investigation were: (1) to describe the habitats present within the study area and clarify how the Snow Partridge utilizes them, (2) to examine the habitat use by this bird and (3) to estimate the potential habitats as a basis for conservation management.

Methods

Study area

The study was carried out in August 2013 in the alpine region of the Balangshan mountains (30°53′–30°57′N, 102°52′–102°54′E) on the eastern edge of the Qinghai-Tibetan Plateau, within the administrative counties of Xiaojin, Wenchuan and Baoxing in Sichuan Province, China (Fig. 1). The Balangshan mountains peak at 5070 m (Liu and Zeng 2011), a high point between the Wolong Nature Reserve to the northeast and the Siguniangshan Scenic Spot to the south. In this region, the tree line varies between 3300 and 3800 m. Below these elevations, the vegetation is dominated by *Abies faxoniana, Quercus aquifolioides, Rhododendron faberi* ssp. *prattii* and *R. asterochnoum*. A zone of shrubs, grassland and sedges, including *Rhododendron nivale*, other *Rhododendron* spp. and dwarf willows (*Salix* spp.), found between 3800 and



4500 m, are disturbed by grazing for domestic yak and horses. Above 4500 m, the habitat consists largely of bare rock (Wolong Nature Reserve Administration Bureau 1987; Cai and Huang 1990; Shi et al. 2000). Glaciers must have been extensive during repeated Quaternary glaciations and many classic features of glacial landforms, appearing above 3800 m (Cao 2004), are found within our study area, including cols, corries, hanging valleys and moraines. Pyramidal peaks and arêtes appear near the top of the mountains above 4500 m (Cao 2004).

The permanent snow line in areas close to our study site appeared between 4600 and 5100 m in 1981-1982 (Liu et al. 1986). At our campsite at 4487 m in August, pre-dawn temperatures dropped below 0 °C with frost and ice on most mornings, and occasional snow flurries by day and by night left sprinklings of hoar that disappeared within a few hours. Climatological data collected in 2009–2010 at 3848 m on the east slope and at 3852 m on the west slope (Liu and Zeng 2011) show that the yearround average temperature is 1.8–1.9 °C. Temperature in the vicinity decreases with elevation by 0.44 °C per 100 m (Wolong Nature Reserve Administration Bureau 1987). The total annual precipitation is 892-1102 mm. Snowfall occurs on 125-141 days per year, mostly between October and April, with March as the month of heaviest snow. Snow cover may last 119 days and increases with elevation by 4 days per 100 m (Liu and Zeng 2011). Within our study area there was one seasonal pool at 4495 m, ephemeral puddles between rocks and apparently permanent streams beginning below 4300 m elevation.

The study area at Balangshan mountains has been strongly affected by glaciations. The mountains are of partially metamorphosed rock originating as subaerial deposits of sedimentary material that has been compressed, uplifted and deformed, so that strata of readily fragmented material are visible at and near ridge lines as vertically standing sheets of rock. These continue to be split and eroded by repeated seasonal freezing and thawing, which ultimately results in a highly fractured landscape of sharp, upright projections downslope; the fragments form mobile screes that flow downhill and are diverted round emergent shoulders of harder material. These shoulders expose more rounded outcroppings of bedrock that remain in situ rather than being disjointed and mobile and, because of their greater stability, they support more vegetation on soils in crevices on their tops and flanks, as well as protecting downslope areas from the scree such that grasses and herbs can proliferate. Mobility of the scree is ensured by continued input of eroded materials from the peaks and ridges above, onto slopes that in places exceed 50° and to a minor extent by the movements of large ungulates that disturb unstable material.

We identified seven habitats and mapped their distribution at the study site.

- (A) Pyramidal peaks: sharp peaks formed where ridges, separating three or more cirques intersect, with steep slopes >60°, appearing above 4600 m. Patches of grass and moss (e.g. *Polygonum viviparum* and *Arenaria bryophylla*) (<5% cover) occur on pockets of soil between rocks.
- (B) Arêtes: narrow, almost knife-edged ridges of rock running down from the angle of a nearby pyramidal peak, appearing above 4400 m. Patches of grass and moss (e.g. *A. bryophylla, Artemisia comaiensis* and *Lilium lophophorum*) (typically 5–20% cover) are found on soil on and between the rocks
- (C) Steep rock slopes: bare rock slopes >60°, forming shoulders and cliffs (defined as any near-vertical face more than 3 m in height) cut by ice, showing up between 4300 and 4600 m. Patches of grass, moss and rosette plants (e.g. *L. lophophorum, Taraxacum* spp. and *Meconopsis integrifolia*) (5–40% cover) occur on soil on and between the rocks.
- (D) Mobile scree slopes: on each side of the arêtes and on steep slopes covered by potentially mobile stone, i.e., detached from the bedrock, the scree consists of individual stones typically <0.5 m, angular, with differential weathering and rounding of some facets. Slopes are often 45°–60° and are prevalent between 4300 and 4500 m. Patches of grass and moss (e.g. *Saussurea* spp., *Anaphalis flavescens* and *Veratrum grandiflorum*) are scanty (<5% cover) showing up on soil pockets between some rocks or are absent altogether.
- (E) Flat or gently sloping rocky areas: these areas, towards the foot of the steep rocky slopes, are covered by big stones (many exceeding 1 m). Such areas appear between 4300 and 4500 m with slopes <45°, although some rocky areas are found below 4000 m. Patches of herbs, grasses and moss (e.g. *Saussurea hieracioides, Taraxacum lugubre* and *Meconopsis* spp.) (5–15% cover) occur on the soil on and between rocks.
- (F) Grasslands: large areas covered by mixed grasses (e.g. *P. viviparum, Ranunculus tanguticus* and *Euphorbia pekinensis*) with other monocots and a range of annual and perennial flowers, occurring between 3800 and 4600 m.
- (G) Shrublands: shrubs appear patchily below 4400 m, but occupy large areas of the valley floor to below 3800 m; these shrublands are dominated by dwarf woody plants such as *Rhododendron* spp., willow (*Salix* spp.) and shrubby cinquefoil (*Potentilla fruticosa*).

In this region, local culture is influenced by Buddhism, in which hunting wildlife is regarded as taboo. The adjacent Wolong Nature Reserve as a good representative for all wildlife being well conserved, is world-famous for the conservation of the Giant Panda (Ailuropoda melanoleuca) particularly. We saw no evidence of hunting of the Snow Partridge; we could observe the partridges down to a 50 m range. Only two people are seasonally resident within our study area, operating a summertime roadside stall. These two, and visitors from nearby villages (e.g. Jelong 26 km from the study site) on numerous days of public holidays, scour the rocky hillsides in search of deep-rooted or fleshy rosette plants with medicinal value. However some level of activities is possible because occasionally people were detected moving on the high slopes long before dawn. A few graziers/pastoral farmers seasonally occupy bothies in the grassland and shrub zone and evidently round up their stock from higher elevations into winter pens, erecting drystone walls and large-mesh wire fences at distant intervals across the landscape. A single road from Jelong to Wolong snakes up on one side of the Balangshan pass and down the other in a series of many hairpins, catering for about 100 vehicles per day, mostly heavy lorries.

Data collection

The area of our study site covered 526 km², a border area of three counties (Fig. 1). Our sampling effort was concentrated within 12 km² of mountain slopes centered around 30°54'39"N, 102°53'41"E. We spent a total of 20 days and approximately 320 man-hours in the field. All suitable habitats in the area were surveyed repeatedly by line transect method. In the mornings when the Snow Partridges left their roosting sites and in the evening when they returned, they called as a group, or called at any time when a predator, e.g. a Red Fox (Vulpes vulpes) or a large herbivore, such as the Domestic Yak (Bos grunniens) or Blue Sheep (Pseudois nayaur) moved close to their sites. Partridges responded to playbacks in the morning. On rainy and foggy days, partridges called periodically during the daytime. The calls revealed the positions of the birds and the open habitat allowed us to approach and locate them precisely from within distances of up to 600 m. We identified the position of the roosting site of each flock by listening before sunrise (at approximately 05:45 h) along the road and existing paths in the area. Playbacks are an effective method for increasing the detection of Galliformes (Wang et al. 2004). The position of each roosting site was marked on a map of the study area. During the daytime surveys, we walked at a speed of 1.5–2.5 km/h, to cover the range of elevations of a specific ecological or plant community between 4000 and 4800 m. Once a partridge flock was detected, we stopped and maintained a distance of >100 m to observe the movements of the flock. We assumed that this procedure was adequate to minimize observer effects. Given that these birds are well protected, without evidence of hunting in the area, the partridges are often undisturbed by people passing with 50 m from their position (Nan Wang, unpublished data). We determined the location of birds, using a hand-held GPS receiver (Garmin GPS12C), once the flock left or, alternatively, we plotted the location on the study area map if the area was too steep for immediate follow-up. We established a 20 m \times 20 m plot (0.04 ha) at flock location and at randomly selected locations with similar features (steep slopes, high elevations, fractured rock or unstable scree) for assessing the habitat features selected by the partridges. For each 0.04 ha plot, we measured the following attributes (Table 1): elevation (m), aspect/direction of slope (measured with a compass), steepness of slope (degrees measured with an altimeter), rock cover (% of the plot lacking vegetation, estimated visually), area of detached rock (% of the plot covered by rocks detached from the underlying bedrock and therefore inherently mobile), vegetation cover (%, estimated visually), highest cliff within the plot (m, a cliff being defined as any near-vertical or overhanging rock face equal to or higher than 3 m), distance from edge of plot to the next nearest cliff (m, distance paced and estimated to next nearest rock face equal to or higher than 3 m) and height of the nearest cliff (m, estimated

Table 1 Habitatmeasurementscollectedatusedand unused locations of the Snow Partridge (Lerwa lerwa)at Balangshan mountains on the eastern Qinghai-TibetanPlateau, Sichuan Province, China

Model variable	Habitat measurements		
x1	Elevation (m)		
x2	Aspect (compass degrees)		
x3	Slope (degrees)		
x4	Rock cover (%)		
x5	Detached rock cover (%)		
хб	Vegetation cover (%)		
х7	Highest cliff (m)		
x8	Distance to nearest cliff (m)		
x9	Nearest cliff height (m)		
x10	Bare ground (%)		
x11	Moss cover (%)		
x12	Grass cover (%)		
x13	Shrub cover (%)		
x14	Other plant cover (%)		
x15	Moss height (cm)		
x16	Grass height (cm)		
x17	Shrub height (cm)		
x18	Other plant heights (cm)		

visually). Within each 0.04 ha plot, we randomly established five 1 m² quadrats and used a 1 m² plastic frame divided into 100 grid squares using thread to estimate the percentage of each quadrat covered by mosses, grass and reeds (Poaceae/Gramineae/Cyperaceae), shrubs, bare ground and other plants (mostly Polygonaceae, Crassulaceae and Primulaceae). We also estimated the average height (cm) of each of vegetation cover.

Data analysis

To determine the micro-habitat variables that Snow Partridges might select, we used a random forests modeling technique, which is a combination of tree predictors such that each tree depends on the values of a random vector sampled independently and with the same distribution for all 'trees' in the 'forest' of possibilities (Breiman 2001). The two indicators, the 'Mean Decrease Accuracy' and the 'Mean Decrease Gini', both refer to the importance of variables; for both indicators the axiom holds that the greater the value the relatively more important the variable. A dichotomous response variable was scored as '1' when a partridge was present in the plot and '0' when the bird was absent. We used 25 presence and 27 absence locations with 18 micro habitat variables for developing the model (Table 1). We implemented the random forests model based on a classification tree using R 3.1.2 for Windows (Li 2013).

In order to examine the habitat selection and model its availability to the Snow Partridge at meso-scale, we used a maximum entropy algorithm (MaxEnt ver. 3.3.3.e) for the three counties (Wenchuan, Xiaojin and Baoxing) adjacent to our main study site, with a total area of 12,800 km² (Fig. 1). MaxEnt finds the distribution of maximum entropy (i.e., closest to a uniform distribution) subject to the constraint that the expected value of each environmental variable (or its transform and/or interactions) matches its empirical average (Phillips et al. 2004, 2006). We included three groups of variables, potentially important for this species, based on our field observations and those of other investigators (Cheng et al. 1978). The first group, referred to as terrain, consisted of elevation, slope (degrees from horizontal) and aspect (compass degrees) from the digital elevation model (DEM) from the Geospatial Data Cloud of the Chinese Academy of Sciences (http://www.gscloud.cn/) (Table 2). The variable aspect, reclassified to eight direction codes as North 1, Northeast 2, East 3, Southeast 4, South 5, Southwest 6, West 7 and Northwest 8, in 45° segments from 0° to 360° clockwise, with 0° and 360° both indicting due north, is a categorical environmental layer in modeling. The second group of variables, referred to and based on distances, consisted of the distance to the nearest ridge, digitized and transformed from ridge lines by the Spatial Analyst Tools of 'Euclidean Distance'. The ridge lines were extracted from a hydrological analysis by the DEM of the Geospatial Data Cloud of the Chinese Academy of Sciences in ArcGIS 10.2 (for details see Tang and Yang 2006). The third group was the land-cover type derived from the National Geomatics Center of China (http://www.globallandcover.com/). All variables were at a resolution of 30 m \times 30 m, within the Projected Coordinate Systems of the Beijing 1954 GK Zone 18 N from the Geographic Coordinate Systems of the WGS 1984. We used the Band Collection Statistics in the Spatial Analyst extension ArcGIS to calculate correlation among the five environmental layers; no variable was eliminated because the highest correlation was only 0.41 between 'ridgedis' and 'vegetation' (r > 0.85; e.g. Lyu et al. 2015, Table 3). Additionally, the size of our field sampling area of only 12 km² may have affected precision of our prediction. However, because there are still no data about the home range of the Snow Partridge, we referred to the 1.02 km movement range of the Tibetan Snowcock (Tetraogallus tibetanus) in elevation (La et al. 2011) as an indication of the potential presence of our partridge. We often observed the Snow Partridge and Tibetan Snowcock together, although the territory of Snow Partridge seemed more limited than Tibetan Snowcock during our field observations.

Table 2 Data sources and description of variables used				
in MaxEnt to model the habitat use of Snow Partridge				
(Lerwa lerwa) at Balangshan mountains on the eastern				
Qinghai-Tibetan Plateau, Sichuan Province, China				

Variable	Description			
Land cover type	Classified based on 30 m resolution Global Land Cover (Globeland30-2010) from National Geomat- ics Center of China (http://www.globallandcover. com/) and include cultivated land, forests, grassland, shrubland, wetland, waterbodies, tundra, artificial surfaces and permanent snow and ice			
Terrain				
Elevation	Elevation above sea level, obtained from http://www.gscloud.cn/			
Slope	Extracted from a 30 m × 30 m digital elevation map (DEM), downloaded from http://www.gscloud.cn/			
Aspect	Extracted from a 30 m \times 30 m digital elevation map (DEM), downloaded from http://www.gscloud. cn/ and reclassified into 8 direction codes: North 1, Northeast 2, East 3, Southeast 4, South 5, Southwest 6, West 7 and Northwest 8, by 45° from 0° to 360° clockwise, with 0° and 360° both indicating due north. Aspect as a categorical environmental layer with 8 categories, used in MaxEnt			
Distance				
Distance to ridge	Ridge map drawn based on ridgelines extracted from a 30 × 30 m digital elevation model (DEM) follow- ing the method of hydrological analysis (Tang and Yang 2006). Distance to ridge is the distance from the locations to the nearest ridge			

Table 3 Correlation coefficients among the five environmental variables for modeling and predicting potential distribution of Snow Partridge (*Lerwa lerwa*) at Balangshan mountains on the eastern Qinghai-Tibetan Plateau, Sichuan Province, China

	Elevation	Aspect	Ridgedis	Slope	Vegetation
Elevation	1.00000				
Aspect	-0.00207	1.00000			
Ridgedis	-0.17068	0.02161	1.00000		
Slope	-0.05896	-0.00021	0.07921	1.00000	
Vegetation	0.40806	-0.01335	-0.08274	-0.01696	1.00000

Ridgedis: the distance of a Snow Partridge flock to the nearest ridge line

We had a total of 86 locations of bird occurrences and after removing locations that were spatially autocorrelated based on a Moran's I analysis with a buffer of 28 m (0.35–0.36; p < 0.05), then we used 71 locations (De Marco et al. 2008) (Fig. 1). Of these 71 locations, 75% were selected randomly as a training set, with the remaining 25% reserved for testing the resulting models (Razgour et al. 2011; Kassara et al. 2014). A logistic output of MaxEnt, with suitability values ranging from 0 to 1, was used (Phillips and Dudík 2008) to represent the logistic probabilities of occurrence. We used the recommended default parameters for the convergence threshold (10–5), regularization multiplier (1), cross-validation during each replicate, with 10 replicates and the maximum number of iterations (500) (Phillips and Dudík 2008; Lu et al. 2012b).

We used receiver operating characteristic (ROC) curves to assess the predictive performance at all possible thresholds (Fielding and Bell 1997). The area under the ROC curve (AUC) has been used extensively as an efficient indicator for measuring the ability of a model to discriminate between locations of presence versus absence in the distribution modeling literature (Hanley and McNeil 1982; Wang et al. 2007). Among the value range from 0 to 1 of AUC, a score of 0.5 implies a predictive discrimination that is no better than random, whereas a score of 1 indicates perfect discrimination and values <0.5 indicate performance worse than random (Anderson et al. 2006). Values above 0.7 were considered to give good model accuracy and reasonable predictions (Aldridge et al. 2008). The 10th percentile training presence logistic threshold, the value above which the model classifies correctly 90% of the training locations, was selected as the threshold value for defining suitable habitats. This conservative threshold is commonly used in species distribution modeling studies (e.g. Raes et al. 2009; Rebelo and Jones 2010; Razgour et al. 2011). Jacknife tests were employed to estimate the apparent importance of the measured variables in estimating potential geographical distributions.

Results

Terrain and habitat use

We found 13 Snow Partridge flocks in the study area on pyramidal peaks, arêtes and steep rock slopes above 4430 m, while no birds were found on mobile scree slopes, flat rocky areas, grass- or shrublands (Table 4). Feathers and feces were found on pyramidal peaks, arêtes, steep rock slopes and nearby sites (not more than 30 m from these habitats) on both north- and southfacing slopes. Roosting sites of six flocks were located at pyramidal peaks and arêtes above 4600 m.

In the mornings, when a group left the roosting site, the birds would fly (1 flock: n = 5 observations) to a lower rocky ridge, or walk down (5 flocks: n = 10 observations) along arêtes or steep rocky slopes to ridges with more ground plant cover, digging for food on the way. Between 9:00 and 17:00, the groups were found at arêtes (5 flocks: n = 11 observations) and steep rocky slopes (4 flocks: n = 7 observations). As a group the birds moved up towards arêtes along the top of mountain ridges after 17:00 (2 flocks: n = 4 observations). The birds dug in the soil for food below the surface and traces of digging, feces and feathers were found on the pyramidal peaks above 4700 m along the ridges to the steep rocky slopes and arêtes at 4350 m, but not in shrubland areas. All detections of foraging were within 30 m of pyramidal peaks, arêtes or steep rocky slopes. When reaching an open area where flat grassland and rocky areas intervened, the birds passed quickly and moved to the next rocky ridges (n = 15 observations). When a fox appeared, the flock members released alert calls till the fox had moved away (n = 2 observations). When the observer moved too close to the birds, the flocks moved away towards or behind rocky ridges (n = 9 observations), glided along steeper cliffs (n = 7 observations), or flew down to lower cliffs (n = 4 observations). Observations on one flock showed that on its daily route, the group often covered the full span of elevations within its home range, from 4400 m near the base of the steep rocky slopes to 4700 m at a pyramidal peak. Between 12:00 and 14:00 the groups were found resting at arêtes (n = 4 flocks) or steep rocky slopes (n = 2 flocks).

Micro-habitat selection

At the micro-habitat scale, distance to the next nearest cliff was ranked the most important environmental variable, followed by the height of cliffs. The elevation and slope angle were the next most important, although their ranking differed depending on the analytical methods used, either the Mean Decrease Accuracy or the Mean Decrease Gini Index (Fig. 2). Vegetation covers such as grass and moss made a moderate contribution to the characteristics of a used habitat. Shrub cover and shrub

Code	Number of encounters	Group size	Range of elevations (m)	Habitat type	Roosting habitat
1	2	40	4553-4700	А, В	
2	1	15	4600	A, B	
3	1	≥5	4653	В	
4	10	40	4500-4700	А, В, С	А
5	1	5	4573	B, C	
6	2	6	4623-4643	A, B	
7	2	Calling and found the droppings	4437-4442	В	
8	2	10	45004600	В	В
9	3	7, 10, 11	4484-4607	B, C	В
10	2	≥5	45504590	В	В
11	2	≥5	4417-4450	В	В
12	1	≥5	4480	В	В
13	1	30	4429	С	

Table 4 Encounters of Snow Partridge (*Lerwa lerwa*) flocks at Balangshan mountains on the eastern Qinghai-Tibetan Plateau, Sichuan Province, China

A habitat of 'pyramidal peak', B'arête', C'steep rock slope'

height seemed to be the least important (Fig. 2). In general, the variables associated with physical structures ranked high, while variables associated with vegetation cover ranked as moderate and those associated with vegetation height ranked low in importance.

Meso-scale habitat selection

The average AUC from MaxEnt for predicting the distribution of the partridges was 0.98 for training and testing, suggesting that the model was able to predict potential



suitable habitats for the Snow Partridge in an effective manner. Of the five environmental variables in the model, elevation showed the highest contribution (AUC > 0.95) and appears to convey the most information for distinguishing suitable habitat. Land cover type (AUC \approx 0.9) made the second greatest contribution to the prediction. Distance to ridges showed moderate contribution (AUC = 0.77), while slope and aspect contributed the least to prediction (Fig. 3).

Potentially suitable habitat

We transformed the probabilities from MaxEnt, calculated as a result of species presence, into predicted presence/absence data. The value 0.2643 of the 10th training percentile was chosen as a threshold to distinguish suitable versus unsuitable habitat (Fig. 1). The area of suitable habitat was about 6.64% (850 km²) of the entire study area (12,800 km²). The threshold of 0.2643 was the maximum value among all available thresholds. Among the others, 0.1248 of the minimum training presence logistic threshold, 0.2416 of the equal training sensitivity and specificity logistic threshold and 0.1544 of the maximum training sensitivity plus specificity logistic threshold, suggest that the ranges of suitable habitats based on the tenth training percentile was between the lowest elevation and the snowline and the nearest approximation to earlier research records (Cheng et al. 1978) and our own field observations. Thus, by contrast, a suitable habitat turned out to be the most conservative and precise prediction. Suitable and predicted habitats for the Snow Partridge appear to be crests of mountain ridge lines, approximately 4200 m and above in elevation.



Discussion

Choice of models

We chose to use the random forests model (Breiman 2001) for analysis of micro-scale habitat selection, and the MaxEnt model (Phillips and Dudík 2008) for the prediction of meso-scale distribution. We regarded the use of MaxEnt as a best single default approach to species distribution modelling since it has been widely used and Elith et al. (2006) found that MaxEnt outperforms other modelling algorithms. However, such results are based on how the fit of the model is evaluated (normally using AUC and ROC) with respect to uncertainties (Diniz-Filho et al. 2009). To evaluate model uncertainties, several indices such as the true skill statistic (TSS), the kappa statistic, the ROC curve and standard deviation are often used to evaluate the model. As described above, we used ROC to evaluate the predictions of the MaxEnt model, which gave a high average value of 0.98, suggesting that the Max-Ent predictions should be robust (Lyu et al. 2015). Dunn (2015) reviewed uncertainty using standard deviation and subtracting that from the respective niche model, and demonstrated the variation in AUC across all Himalayan Galliformes. There is a clear tendency amongst ecologists to use combined predictions under the "ensemble forecasting approach" proposed by Araújo and New (2006) and Diniz-Filho et al. (2009). Marmion et al. (2009) have also evaluated consensus methods as much variance in SDMs may come from different modelling algorithms.

Rather than using ensemble forecasting, by running different modelling methods and combining projections to obtain a consensus projection (Araújo and New 2006; Thuiller et al. 2009, 2016), we favored an approach using random forest at micro-scale and confining MaxEnt predictions only to the three counties from within which our locations are samples. We are not confident that habitat selection is uniform throughout the Snow Partridge's range, and recommend that ensemble forecasting using consensus methods such as BIOMOD2 (Lu et al. 2012a; Thuiller et al. 2016) should be applied when larger datasets are available and modelling can be applied across the entire species range.

Habitat selection

During our field survey, confined to the post-breeding period, 13 flocks of partridges were found on pyramidal peaks, arêtes and steep rock slopes at elevations above 4430 m. We did not find any birds at lower elevations. Vertical movement of the birds covered the range from 4430 m, the lowest point of their activity on any day, to 4700 m, the highest elevation at pyramidal peaks, where they roosted. In comparison, previous surveys by Lu (1988) and Lu et al. (1989) found Snow Partridges on rocky alpine zones at elevations ranging from 4100 to 4400 m in Wenchuan (Lu et al. 1989) and from 4000 to 4200 m in Baoxing (Lu 1988); their 1989 study also reported two nests found at 4150 m under rocks and their 1988 study reported nests at 3800 m on the grassland. The differences between our survey results and these earlier studies are probably caused by local variations in elevation of various habitat types according to topography and climate, and the fact that the habitat at lower elevations of grassland provided adequate food for meeting the needs of foraging during the breeding season. Another factor might be global warming, which has led to a more rapid retreat of glaciers, ice and snow cover in the Himalayas than the world average. Xu et al. (2009) recorded an upward and northward movement of the tree line; particularly in the eastern Himalayas the tree line moved 100 m during the past century.

Our results suggest that physical landform is an important factor for habitat selection of the Snow Partridge. The partridge stayed at the tops of high cliffs or flatter terrain close to high cliffs, on more gentle slopes and high elevations above 4300 m. Our own observation indicated that these features would facilitate predation avoidance of partridges for gliding from steep cliffs.

Potential predators at the study area include large raptors e.g. the Common Buzzard (Buteo buteo) and the Golden Eagle (Aquila chrysaetos), although very few were seen in August. At lower levels, tracks of the Red Fox, Weasel (Mustela sibirica) and a suspected Leopard Cat (Prionailurus bengalensis) were seen. By comparison to predators, vegetation cover types and plant height seemed to rank low in importance (Fig. 2); still, much of this landscape could provide dietary sources such as moss, lichen, berries, shoots and seeds (Cheng et al. 1978). At a microscale of a few meters, vegetation clusters and tussocks among rocks, suitable for partridge foraging, were commonly available except on the most exposed peaks and the most unstable screes. Variables of land-cover types played important roles in predicting suitable habitat at a meso-scale (tens to hundreds of meters), in which grassland contributed the most (Fig. 3). Our 'grassland' type included a wide taxonomic and morphological array of plants including reeds, mosses, rosette and cushion forming angiosperms, which could provide the birds with refuge from danger, food, nesting shelter and nesting material (Cheng et al. 1978; Li 1986) (Figs. 3, 4b). Terrain and vegetation structure have been identified as key factors at different scales in habitat selection among various Galliformes such as Cabot's Tragopan (Tragopan caboti) (Ding and Zheng 1997), Golden Pheasant (Chrysolophus pictus) (Shao 1998), White Eared-pheasant (Crossoptilon crossoptilon), Blood Pheasant (Ithaginis cruentus) (Jia et al. 2005) and Reeves's Pheasant (Syrmaticus reevesii) (Xu et al. 2006, 2010). During our study, scale effects clearly showed that topographic factors affect birds at the micro-habitat level while vegetation structures do so at the meso- or macro- habitat level, given the results of the random forests and the MaxEnt models (Figs. 2, 3).

Elevation was a key factor at both scales, suggesting that the Snow Partridge is, to a great extent, highly dependent on elevation and clusters at peaks, ridges and arêtes with highly fragmented rocks. As well, distance to ridge appeared to be an important factor for suitable habitat prediction (Fig. 3). The Snow Partridge favors ridges and peaks, since such high terrain and wider vistas help in detecting predators. It seems evident that, based on our direct observations of the birds and on information from GPS locations at a micro-scale of several meters, Snow Partridges are limited to high elevations where the terrain is largely bare and inevitably steep, but within these landscapes they spend their time in the less steep areas above cliffs, on shoulders of rock, or more gentle open terrain at the foot of slopes where tussock vegetation is more abundant. At meso-scale the preference for ridges, peaks and steep terrain, where the partridge occurs at the top of cliffs or on flatter stony ground confirms the summary descriptions reported by Cheng et al. (1978) and Li (1986). The partridges tended to select sunny slopes (aspect to the east, southeast, south, southwest and west, Fig. 4e, 3-7), as indicated by Cheng et al. (1978). Plant growth as a food resource is likely to be more profuse on sunny southern slopes than in shady areas above 4000 m. At the meso-scale, an elevation and landscape-dependent scale, our partridges were often present on shrubland and grassland feeding on alpine shrubs, plants or mosses with other birds (Cheng et al. 1978; Lu 1988). This suggests that habitat selection by L. lerwa is, in fact, a tradeoff between food availability and predation risk. Yan et al. (2010)carried out a study on brooding site selection by the Himalayan Snowcock (Tetraogallus himalayaensis) and concluded that the environments selected, i.e., those with tall shrubs, rich vegetation, a heterogeneous surface with a number of 500 m cliffs, are a trade-off between food security and avoiding predators. The case of the Snow Partridge appears similar. As an endemic species on the Qinghai-Tibetan Plateau, the habitat selection and distribution of the Snow Partridge suggest an adaptive behavior or a life strategy of birds living in severe cold condition at high elevations.

Based on the results of our environmental niche modeling, we conclude that only 6.64% of the land area of the three counties of Xiaojin, Wenchuan and Baoxing represents habitat suitable for the Snow Partridge (Fig. 1). Despite the almost total lack of human interference with the Snow Partridge, its nearly bare alpine habitat is fragile and, once destroyed, will be difficult to restore and the partridge will face the risk of extinction. While climatic variables have not yet been mapped or analyzed, any climate change leading to the upward expansion of vegetation zones would have obvious consequences for the extent and continuity of suitable habitats and for the conservation of Snow Partridge populations.

MaxEnt could be a useful tool in searching for suitable partridge habitat to guide future field work effectively (Guisan et al. 2013). However, 'MaxEnt is a statistical model and to apply it to model species distribution successfully, we must consider how it relates to two other modeling components (the data model and the ecological model)' (Phillips et al. 2006). That said, MaxEnt is not only a statistical model or an ecological model, but also a data model. But the premise is that SDMs are based on statistics, therefore the model is not a complete simulation of real habitat. As well, it should be recalled that, according to Engler et al. (2004) and Hernandez et al. (2006), statistical models, as a simple calculation of the potential distribution of a species, are not a substitute for field investigation, but a useful tool for data detection, to help identify potential knowledge gaps and to provide guidance for the design of field surveys for rare species (Guisan and

Response of Snow Partridge to elevation

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b

Thuiller 2005; Elith and Leathwick 2009; Guisan et al. 2013). Our study involved a sampling period of only one season and one month at that, with a sampling area of only 12 km² as far as we could reach. Given the difficulty of field work on the Qinghai-Tibetan Plateau with

its snow melting period and hard-walking terrain, our results could be biased and affect the accuracy of prediction, in spite of the extraordinarily high predictive performance with 0.98 of the AUC value in MaxEnt. Hence during any future work, habitat investigations of the Snow Partridge and conservation measures should expand to include a greater survey area and more time from which our current study, with its basic steppingstone results, might have benefitted.

Conclusions

On the basis of our field work, we conclude that movements of the Snow Partridge covered a 300 m range in elevation, i.e., from 4400 m at the lowest point of its daily activity, to its roosting sites at 4700 m, the highest level of pyramidal peaks. Elevation was significantly associated with habitat selection of this partridge, which has adapted to living on this plateau, both on a micro- or meso-scale in three counties. The scale effect was clear evidence of the effect of topographic features where the birds avoid predators at the micro-habitat level and use the vegetation structure at the meso-habitat level for food. Habitat selection of this partridge is a trade-off between predator and prey. To access food sources, they need to leave bare but relatively safe ridgetop roost sites and walk downhill while foraging. On the other hand, they have to move upwards to roost at ridge locations with open vistas easy for gliding should they encounter natural enemies (Cheng et al. 1978). This is the same cycle employed by the other high elevation pheasant, i.e., the Himalayan Snowcock (Yan et al. 2010). Habitat selection by the Snow Partridge is an adaptive strategy under the severe conditions prevailing at high elevations on the Qinghai-Tibetan Plateau.

Authors' contributions

HY analyzed the data of micro-habitats by random forests, modeled Max-Ent and was a major contributor in writing the manuscript. NW conceived, directed and coordinated this study and was one of the parties that surveyed the Snow Partridge, collected field habitat data, helped with writing and revised the manuscript. CD conceived, directed and coordinated this study with NW, provided his guidance and comments for data analysis and the manuscript. GD conducted field work with NW and made contributions in writing the manuscript. YW gave his comments on data analysis and helped write the manuscript. All authors read and approved the final manuscript.

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Competing interests

The authors declare that they have no competing interests.

Availability of data and materials

The datasets generated during our field survey and analyzed during the micro-habitat are not publicly available owing to the fact that they are part of our field work, but are available from the corresponding author on the basis of a reasonable request. Environmental data, used during our MaxEnt modeling

and the Digital Elevation Model (DEM) are available at public networks of the Geospatial Data Cloud of the Chinese Academy of Sciences (http://www.gscloud.cn/) and land-cover types derived from the National Geomatics Center of China (http://www.globallandcover.com/).

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