Crested Ibis in a Dynamic and Increasingly Human-Dominated Landscape

Yiwen Sun

CRESTED IBIS IN A DYNAMIC AND INCREASINGLY HUMAN-DOMINATED LANDSCAPE

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DISSERTATION

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on account of the decision of the graduation committee,
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This thesis is approved by

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Dr. Tiejun Wang, co-promoter

To my beloved parents and husband

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Chapter 1

General Introduction

1 General introduction

1.1 Background

With the exponential growth of human populations over the past centuries, and the consequent demand on natural resources, the Earth is being transformed from large expanses of natural vegetation into a patchwork of natural, modified and man-made ecosystems (Skidmore 2002). Wildlife species have suffered reductions worldwide in population size and geographical range, due to habitat loss, fragmentation and degradation as well as intensive persecution, massive hunting and pollution (IUCN 2007; Li et al. 2009; Deinet et al. 2013). Many species are disappearing off the face of the earth, and many species have been driven into corners where they can hide and live a secret life in marginal and fragile areas (Deinet et al. 2013).

Increasing efforts have been made by local governments, conservation organizations, research institutions and private individuals to preserve and restore the endangered species and their habitats. There are a variety of methods currently being implemented; the most common are creation of protected area networks, captive breeding and reintroduction, conservation legislation, and increased public awareness. Successful conservation projects and strategies have led to the remarkable recovery of some mammal and bird species, even from the brink of extinction, such as the black-footed ferret (*Mustela nigripes*) and peregrine falcon (*Falco peregrinus*) in North America as well as the European bison (*Bison bonasus*) and white-tailed eagle (*Haliaeetus albicilla*) in Europe (Deinet et al. 2013; Newton 2014). However, current conservation efforts remain insufficient to offset the pressures on species, habitats and ecosystems (Hoffmann et al. 2010), and these conservation successes are overshadowed by more species declines and extinctions (IUCN 2015).

Conservation efforts have mainly focused on the protected areas. Species dependent on habitats outside protected areas have to cope with the direct pressure of human disturbance, and the indirect pressure of habitat modification (Olupot et al. 2010). However, conservation management is hampered by lack of information and knowledge about the distributions of species and habitats as well as factors influencing their distributions in these areas (Skidmore 2002). On the other hand, protected areas do not

necessarily guarantee conservation effectiveness. For instance, a flagship protected area for the world-renowned endangered giant pandas in Southwest China was found to be more fragmented and less suitable for giant panda habitation after the reserve was created (Liu et al. 2001). Wildlife populations in protected areas may still be affected by exposure to incompatible land uses such as agriculture, livestock grazing, logging and mining (Skidmore 2002). More challenges can be encountered in the face of the dilemma of balancing biological conservation against exploitation for human production systems (Nagendra 2008). This is particularly true for animal species that only survive within a narrow range of resource requirements in a human-dominated landscape. In addition, a lack of understanding of the ecological requirement as well as habitat availability and suitability of the target species has also attributed to the failure of many reintroduction attempts (Armstrong and Seddon 2007).

Developing a comprehensive conservation strategy requires conservation scientists and managers to simultaneously understand patterns and processes of landscape change, such as alteration and loss of habitat, as well as detailed responses of species to these modifications over geographical space and time (Collinge 2001). The importance of space and time in the relationship between species and environment has increasingly been recognized by ecologists, evolutionary biologists and conservation biologists. They have more fully appreciated the potential effects of surrounding landscape on species at local sites (Gutzwiller and Riffell 2007). The perspective of landscape is improving understanding of the broad-scale factors that influence species distribution, population dynamics and habitat use (Gutzwiller and Riffell 2007). Moreover, the importance of the past in understanding the present and future has been increasingly emphasized, as current ecological phenomena are influenced by the past events and processes (Wiens and Donoghue 2004). On the other hand, dynamic landscape and animal populations can also lead to temporal variation in species-environment relationships (Gutzwiller and Riffell 2007).

Current data on the distribution, status and ecology of wildlife species are generally not available in many regions of the world. Conventional ground-based survey techniques are very costly, labour-intensive and time-consuming across large areas and over time. Moreover, field observation is only valid for locally specific patterns of species and habitat distributions as well as species-environment relationships, which need to be scaled up in space and time. Remote sensing and geographical information systems (GIS)

techniques offer great potential for an analysis or modelling approach to investigate wildlife and its habitat over space and time. Remote sensing has produced a wide range of geospatial datasets and analytical algorithms for mapping biogeographical heterogeneity. GIS can be effective in geospatial analysis and modelling species distribution if the necessary data are available. Over the last few decades, correlative species distribution models (SDMs) have been widely employed to understand the spatial pattern of the relationship between species occurrence and the biotic and abiotic environment at multiple scales in space and time (Elith and Leathwick 2009). Integration of these technologies has been successfully applied in conservation biology and management for many endangered species (Gottschalk et al. 2005; Parviainen et al. 2013; Wilson et al. 2013; Porfirio et al. 2014). Such species occurrence has been identified as an essential biodiversity variable (EBV) by Pereira et al. (2013), while Skidmore et al. (2015) further emphasized species occurrence as a key EBV that requires remote sensing for spatial and temporal models.

1.2 Crested ibis and research problem

1.2.1 Historical population decline of crested ibis and plausible causes

The Asian crested ibis (*Nipponia nippon*), also known as the Japanese crested ibis (hereafter called simply crested ibis), is a medium-sized wading bird. It is one of the most evolutionarily distinct and globally endangered avian species in the world (BirdLife International 2012; Jetz et al. 2014) and ranks as a first-class protected species by national government of China (Harris 2008). The crested ibis was originally widespread in the East Asia, China, Japan, the Korea Peninsula, and the Russian Far East. In China, the bird used to be locally common in a dozen provinces in East and Midwest China (BirdLife International 2001). A large population of crested ibis still inhabited Shaanxi Province in the early twentieth century (Shi and Cao 2001; Ding 2004). Unfortunately, the population of the crested ibis has severely declined since the mid-twentieth century. This species was even evaluated as extinct in the wild when the last five wild birds in Japan were caught and kept into captivity in 1981. However, the captives died without successful reproduction (Ding 2004; Yang 2004). In China, no occurrence of crested ibis was recorded for nearly 20 years after a single specimen was collected in Gansu Province in 1964. In 1981, a tiny wild population of seven birds, two

pairs and three fledglings, was rediscovered in Yang County of Shaanxi Province, China (Liu 1981).

The possible causes of the rapid population decline have been summarized as follows (Shi et al. 1991; Shi and Cao 2001; Ding 2004; Li et al. 2009): 1) the use of pesticides in rice fields not only diminished the food resources of crested ibis, but also led to accumulation of chemical contaminants in the body and consequently to reproductive failures; 2) traditional farming practice keeps the fallow rice fields flooded during winter, while crop rotation dries up the rice fields in other seasons to plant other crops such as winter wheat and rapeseed; conversion of single to double cropping decreased winter-flooded rice fields as foraging habitat for crested ibis; 3) the increased extent and intensity of human activities, especially hunting; 4) deforestation of pine woodlands, especially near farmlands and villages, reduced the availability of nesting and roosting sites; 5) drying up of winter-flooded rice fields as well as natural or semi-natural wetlands due to climate change reduced food resources of crested ibis.

1.2.2 Current status and conservation

For the sake of the only surviving crested ibis population, many *in-situ* conservation measures have been taken to preserve and restore the wild population, including legal protection, establishing a Nature Reserve, protecting forests for nesting and roosting, maintain and restoring winter-flooded rice fields for foraging, controlling environmental pollution, as well as monitoring the behaviour of wild crested ibis (Xi et al. 2002; Zhang and Ding 2008). After 30 years of conservation, the population size of wild crested ibis now exceeds 1000 individuals in 2012 (Wang et al. 2014). Thanks to the steady progress in conservation, the crested ibis has been downlisted from the Critically Endangered to Endangered category. In recent years, the birds tend to move into new nesting sites at lower elevations (Zhai et al. 2001). The geographical distribution of the crested ibis has increased from <100 km² to >3000 km² (Lu et al. 2006; Ding 2010). However, the population viability may be restricted by the carrying capacity of the limited habitat (Li and Li 1998). In addition, if unexpected diseases or natural disasters occur, the isolated population is likely to be confronted with devastating consequences. Following the success of captive breeding programmes, captive-bred birds have been used to reintroduce this species to parts of its former range in China and Japan to reduce the risk of extinction (Yamagishi 2009; Yu et al. 2009).

1.2.3 Limitation in the research and knowledge gap for conservation planning

Unfortunately, apart from a few localities of historical distribution, little was known about the crested ibis before it was on the brink of extinction. The knowledge about this species is largely improved based on the relict population, with respect to reproductive ecology (Yu et al. 2006), habitat use and selection (Ma et al. 2001; Liu et al. 2003; Li et al. 2006), population dynamics and demography (Li and Li 1998; Wang and Li 2008) and conservation strategies (Xi et al. 2002; Su 2008). The studies on species-environment relationships of the crested ibis were based on empirical data as well as over a small extent (where the population were confined in the initial phase of recovery).

For most endangered species, their chance of recovery depends on whether their critical habitat is identified and protected and/or restored. Given the strict conservation, food availability has been identified as the primary limiting factor to the population growth of the ibis (Xi et al. 2002; Yu et al. 2006). Traditional rice farming has provided essential foraging habitat for crested ibis, but is becoming obsolete with the development of modern agricultural technologies as well as the change in land-use policies (Liu et al. 2008). The current conservation policy therefore focuses on maintaining the traditional practice of winter-flooding of rice fields and compensating the farmers for their consequent loss of income. Lack of information on the distribution of winter-flooded rice fields presents a challenge to the conservation management as well as research on habitat evaluation for crested ibis (see Li et al. 2002). Moreover, it is also unclear whether the remaining winter-flooded rice fields have been effectively protected or to what extent they have changed in the past few decades.

In the early stage of the population recovery, almost all the researchers and conservationists interested in the crested ibis, as well as the local authorities and local community, thought that crested ibis distribution was closely related to the presence and abundance of winter-flooded rice fields, especially during breeding season (Wang, Zhao, et al. 2000; Li et al. 2001; Ding 2004; Zhang et al. 2008). As the population increased in size, the crested ibis has been expanding its range from the mountains down to the human-occupied floodplain where traditional farming practice is rare. This raises the question as to how the crested ibis has responded more recently to the distribution of winter-flooded rice fields, particularly because species-

habitat relationships may vary over time and space (Wiens 1989; Li et al. 2006).

Currently, the majority of the wild population is still confined to a relatively small region and its future status is uncertain. As an endangered but recovering species, population increase and range expansion may pose a challenge for its conservation, especially from conflict with humans (Ding 2004; Marucco and McIntire 2010). The accurate predictions of potential habitat and range dynamics has interested conservation biologists based on their desire to identify where this species will be in the future, and are therefore imperative to plan its recovery with respect to the selection of potential reintroduction sites. Range expansion is a highly dynamic process, not only determined by the interplay of demographic and dispersal phenomena, but also by biotic interactions and abiotic landscape influence, such as habitat availability and fragmentation (Hastings et al. 2005; Kubisch et al. 2014). Therefore, modelling species range expansion requires a combination of analysis of spatial landscapes, and knowledge of animal behaviour and population dynamics. Furthermore, understanding the impacts of demographic factors and habitat suitability on range dynamics of crested ibis could also facilitate the conservation management.

However, it is worth noting that the current geographical range of the crested ibis only reflects a snapshot view of the expected species-environment relationship. This relationship may change significantly as a response to changing environmental conditions through time (Nogués-Bravo 2009; Stigall 2012), and does not allow an estimation of the fundamental environmental requirement (Maiorano et al. 2013). A better understanding of species distribution and its environmental requirements in the past prior to widespread human disturbance is essential to inform us about the current state of the species and its potential response to future environmental change (Kuemmerle et al. 2012; Clavero and Hermoso 2015). Historical information on crested ibis distribution has however not been fully taken advantage of in research and incorporated in conservation strategies. Moreover, broad-scale patterns and determinants of crested ibis distribution can provide valuable insights into its response to a changing environment, but have not been understood yet. Climatic and land-use changes have been shown to alter species' geographical distributions (e.g., Ficitola et al. 2010; Auer and King 2014; Gillings et al. 2015), and therefore should be considered as important factors in conservation plans for crested ibis.

1.3 Research objectives

Taking the crested ibis, a charismatic endangered species, as our focal species, the general objective of this thesis is to investigate the spatial response of species to a changing human-dominated landscape. To achieve this, four specific objectives are designed as follows:

- To map and monitor the critical foraging habitat (winter-flooded rice fields) for crested ibis using remote sensing and GIS techniques
- To investigate the associations between spatial patterns of crested ibis and winter-flooded rice fields
- To understand the spatio-temporal dynamics of crested ibis in a heterogeneous landscape
- To establish the historical distributions of crested ibis in geographical and ecological space and to predict its potential distribution under future environmental changes

1.4 Study area

Figure 1.1 Location of study areas at the continental level (East Asia), the regional level (area centred around the current range of the wild crested ibis with a radius of 700 km), and the local level (current range of the wild crested ibis).

Considering the specific research objectives and the availability of materials, this research was conducted within different, unique ranges of spatial and temporal scales with the corresponding spatial extents (Fig. 1.1). In general, three different spatial scales, from local, to regional, and to continental, and three different temporal scales, from the past, to the present, and to the future, are considered. At a local level, the study focuses on the range of the relict crested ibis population in Yang County, Shaanxi Province, China, and the current and recent status and distribution of crested ibis and its habitat since the 1980s after the rediscovery of the relict population. At a regional level, the study looks at the range expansion of crested ibis in the next 50 years within a study area centred around the current range of crested ibis with a radius of 700 km. At a continental level, the study area covers the entire distribution range of crested ibis documented in history, including the Russian Far East, China, Japan and the Korean Peninsula. Meanwhile, the distribution of suitable areas for crested ibis is investigated at three time frames, ranging from the beginning of the 20th century prior to the severe decline of crested ibis population, to the present, and to the end of the 21nd century.

1.5 Outline of the thesis

This thesis consists of six chapters, a general introduction, four core chapters and a synthesis. Each core chapter has been prepared as a stand-alone research paper that has been published in or submitted to a peer-reviewed, international journal. The structure and content of these research papers are largely retained in the thesis. The bibliographic references of each chapter are combined and listed at the end of the thesis.

Chapter 1 presents the research background, research problem, and research objectives, describes the study area and outlines the structure of the thesis.

Chapter 2 applies innovative remote sensing and GIS techniques to map the critical foraging habitat for crested ibis, assesses the change in distribution and extent of this habitat in protected and non-protected areas over the last two decades, and examines the potential impact of this change on the population growth of crested ibis.

Chapter 3 uses the information on satellite-derived distribution of winter-flooded rice fields to explore the relationship between the distribution and

extent of this critical foraging habitat and the nest site distribution pattern of crested ibis.

Chapter 4 predicts the natural range expansion process of the wild crested ibis in a heterogeneous landscape during the next 50 years using a hybrid model integrating habitat suitability and population dynamics, and evaluates the impact of species' life-history traits on the range dynamics.

Chapter 5 establishes baseline information on the historical distribution of crested ibis and its niche characteristics, and predicts the potential distribution under future climate and land-use changes.

Chapter 6 provides an overview of the research findings from previous chapters relevant to specific research objectives to understand the spatial response of crested ibis to a changing human-dominated landscape. The implications of these results for the conservation management of crested ibis are discussed.

Chapter 2

Decline of Traditional Rice Farming Constrains the Recovery of the Endangered Crested Ibis

This chapter is based on: Sun, Y., T. Wang, A.K. Skidmore, Q. Wang, and C. Ding. 2015. Decline of traditional rice farming constrains the recovery of the endangered Asian crested ibis (*Nipponia nippon*). *AMBIO* 44: 803-814.

2 Decline of traditional rice farming constrains the recovery of the endangered crested ibis

Abstract

Traditional agriculture benefits a rich diversity of plants and animals. The winter-flooded rice fields in the Qinling Mountains, China, are the last refuge for the endangered crested ibis, and intensive efforts have been made to protect this anthropogenic habitat. Analyses of multi-temporal satellite data indicate that winter-flooded rice fields have been continuously reduced across the current range of crested ibis during the past two decades. The rate of loss of these fields in the core-protected areas has unexpectedly increased to a higher level than that in non-protected areas in the past decade. The best fit ($R^2 = 0.87$) numerical response model of the crested ibis population shows that a reduction of winter-flooded rice fields decreases population growth, and predicts that the population growth will be constrained by the decline of traditional winter-flooded rice fields in the coming decades. Our findings suggest that the decline of traditional rice farming is likely to continue to pose a threat to the long-term survival and recovery of the crested ibis population in China.

2.1 Introduction

Traditional agriculture incorporating biodiversity-friendly farming practices benefits a rich diversity of plant and animal species in many parts of the world (Czech and Parsons 2002; Wright et al. 2012). Winter-flooded rice farming is a traditional agricultural method that involves single cropping and then flooding the fallow field during winter to ensure the water supply for the next year. Conservation scientists and practitioners have widely recognized that these flooded rice fields provide alternative or complementary foraging habitats for waterbirds during the winter and breeding seasons (Elphick 2000; Wood et al. 2010; Toral et al. 2011).

The crested ibis (*Nipponia Nippon*) was once widespread across East Asia, including Japan, China, Russia and the Korean peninsula, but it is now extinct over almost all of its former range (BirdLife International 2012). The last seven individuals were discovered in 1981, in a remote village on the southern slopes of the Qinling Mountains in China (Liu 1981). Their refuge comprised several ancient oaks for nesting and nearby winter-flooded rice fields for foraging (Schaller 1994). Apart from a few records of the historical distribution of this species, previous studies on reproduction (Yu et al. 2006), foraging and breeding habitat selection (Ma et al. 2001; Liu et al. 2003), population dynamics and demography (Wang and Li 2008) and conservation strategies (Xi et al. 2002; Su 2008) in wild crested ibis have been conducted based on this rediscovered and recovering population. Scientists attributed the dramatic decline of the crested ibis population in the mid-twentieth century to the combined influence of habitat loss (due to changing farming practices) and the high risk of human-induced mortality (due to hunting and use of toxic pesticides) (Ding 2004; Li et al. 2009). Consequently, intensive conservation efforts have been made to prohibit hunting and deforestation, to monitor the nesting habitats, to prevent predation, and to limit or prohibit the use of agrochemicals over the past 30 years (Xi et al. 2002; Su 2008). It is commonly believed that the strict conservation measures combined with a higher public awareness contributed to increased breeding population size and reduced anthropogenic disturbances, which have contributed to the rapid recovery of the crested ibis population (Wang and Li 2008). Given such strict conservation, food availability has been identified as the primary limiting factor to the population growth of the ibis (Xi et al. 2002; Yu et al. 2006).

Although semi-natural or natural wetlands in the floodplain may function as alternative habitats for the crested ibis during the post-breeding season (July to October), adult birds in the montane areas exclusively forage in the winter-flooded rice fields during the winter and breeding seasons (Ma et al. 2001; Liu et al. 2003). Additionally, a principal component analysis by Wang, Zhao, et al. (2000) and a resource selection analysis by (Li et al. 2001) indicated that the proximity as well as area of winter-flooded rice fields was an important factor in selecting nest sites by crested ibis. The winter-flooded rice fields have served as essential habitats for the survival and recovery of the crested ibis population over the past 30 years (Ding 2004). Loss of these habitats may lead to food shortages for the crested ibis population, particularly in the winter and breeding seasons. Therefore, considerable efforts have also been made to maintain and restore the winter-flooded rice fields for the conservation of this endangered species, especially in the core-protected areas. For example, the Chinese conservation management agency signed agreements with local farmers to maintain the traditional farming practice and promoted ecological compensation to offset the incurred losses (Ding 2004). Since 2001, the birds have dispersed and established more and more nest sites outside the protected areas; their distribution area is now 30 times larger than the 100 km² in the 1980s and early 1990s (Ding 2010). However, this means that limited financial and human resources have to be shared across a much larger area, so that effective conservation management of the winter-flooded rice fields is likely to become more difficult.

Traditional farming in China is becoming obsolete with the development of modern agricultural technologies as well as the change in land use policies (Liu et al. 2008). For example, since 1960 the construction of reservoirs has led to better agriculture and irrigation conditions and has addressed the problem of supplying enough water for rice production. With the introduction of double cropping, the winter flooding of rice fields has been increasingly replaced by dryland farming of rapeseed or winter wheat. This change in farming practice was further stimulated by the rapid growth in demand for grain under the pressure of an increasing human population. Between the 1950s and 1980s the winter-flooded rice fields in the floodplain of the Han River decreased by almost 90% (Dong et al. 1992).

For most endangered species, their chance of recovery depends on whether their critical habitat is identified and protected and/or restored. Thus, monitoring the spatiotemporal change of winter-flooded rice fields plays a

fundamental role in both agriculture and conservation. Unfortunately, it is unclear whether the remaining winter-flooded rice fields in the distribution area of the crested ibis have been protected or to what extent they have changed in the past two decades, as well as the ecological impact of these changes. Scientists, conservation managers and agencies are unable to conduct these studies because of a lack of appropriate technology, methodology and funding. This is where remote sensing methods can be a time- and cost-effective alternative. A number of studies have demonstrated the use of multi-temporal remotely sensed data for monitoring changes in rice agriculture on a large scale (Gumma et al. 2011; Moré et al. 2011), as well as for assessing the dynamics of flooded rice fields available to waterbirds in flat and homogenous landscapes (Fleskes et al. 2005; Toral et al. 2011). Integrated remote sensing and GIS techniques can yield precise spatial information on the distribution of scattered winter-flooded rice fields and any subtle changes (Sun et al. 2014).

Taking the current range of the crested ibis as an example, we assessed the changes of winter-flooded rice fields in protected and non-protected areas over the last two decades, and examined the potential impact of these changes on the population growth of crested ibis. Our specific objectives were to: (1) identify the changes that have taken place to winter-flooded rice fields, (2) compare the magnitude of changes in these fields between the core-protected and non-protected areas, (3) investigate the mechanism for the population growth of crested ibis under the change of winter-flooded rice fields and forecast future population trends.

2.2 Methods

2.2.1 Study area

The study area is located on the southern slopes of the Qinling Mountains in the central area of Yang County, Shaanxi Province, China (Fig. 2.1). It encompasses 1080 km², centred at 33°19'N and 107°33'E, and covers an elevation range between 425 m and 1909 m. In 2009 about 80% of all known nest sites of the crested ibis were established in this area. Major land cover/use (hereafter called simply land use) types in the study area include forest, shrub, grass, cropland, open water, built-up areas and waste land. The cropland can be divided into rain-fed fields with dryland crop cultivation, summer-irrigated rice fields with a dry fallow period or

rotational dryland cultivation in winter (winter-dry rice fields), and rice fields with an intentionally or naturally flooded fallow period from October to May (winter-flooded rice fields).

Figure 2.1 Map of the study area. The locations of nest sites in 1981 (triangle) and 2009 (dots) are marked. Three specific study areas with a radius of 3.5 km are located at the original nest site in 1981 (Area 1), the area with the highest nest site density (Area 2), and the new location of nest dispersion outside the core-protected area in 2001 (Area 3). The boundary of the protected area is outlined with a white dotted line.

Special attention was paid to three areas when we considered the distribution of both the crested ibis nest sites and winter-flooded rice fields (Fig. 2.1). The first area is centred at the original nest site that was discovered in 1981. The second area had the highest density of nest sites. The local authority claims both are in the core area and are under strict

protection. The third area was centred around the first nest site that was established outside the core-protected areas. Long-distance dispersal to non-protected areas first took place in 1999 (Ding 2010), and more nest sites have been established around the third area since 2001. Temporal changes of the crested ibis population in the whole study area and the number of nest sites in the three specific areas are presented in Fig. 2.2. Previous studies found that the foraging distance of the crested ibis in winter and breeding seasons rarely exceeds 3 km on average (Liu et al. 2003). We therefore chose a radius of 3.5 km for our study areas. The elevations of the three areas decrease successively, while the human population density increases, from Area 1 to Area 3.

Figure 2.2 Temporal changes of the crested ibis population in the whole study area and number of the nest sites in three specific areas from 1988 to 2009.

2.2.2 Classification of winter-flooded rice fields and associated major land use types

Preparation of satellite images and ancillary topographic data

We used Landsat images to map the distribution of winter-flooded rice fields and the associated major land use types at a spatial resolution of 30 m. Six orthorectified Landsat images were downloaded from the U.S. Geological Survey Earth Explorer site (<http://earthexplorer.usgs.gov/>), namely, Landsat Thematic Mapper (TM) (28/08/1987, 20/12/1988, 30/07/2000, 12/01/2009, and 05/06/2009) and Enhanced Thematic Mapper Plus (ETM+) (14/11/2001). The multi-season cloud- and snow-free images were needed to identify the flooded areas in winter and the mixture of surface water and rice plants during the growing season around 1988, 2001 and 2009, respectively. The Landsat images were geometrically rectified using 1:50 000 topographic maps and the processing utilized a second-order polynomial and nearest neighbour interpolation with an accuracy of less than 0.5 pixels (15 m) root mean square error. The TM/ETM+ bands 1-5 and band 7 (thermal band 6 was excluded) in two scenes in three time phases were stacked and reprojected to UTM zone 48N, datum WGS84. All image pre-processing was executed using ENVI 4.8.

Topographic information, including elevation and terrain position (i.e., gully, lower mid-slope, mid-slope, upper mid-slope and ridge), was derived from 30-m ASTER Global Digital Elevation Model (DEM) with vertical accuracies between 10 m and 25 m RMSE (<https://lpdaac.usgs.gov/>). The DEM data were geometrically co-registered with the Landsat images using a second-order polynomial and nearest neighbour interpolation. Five terrain position classes were calculated using the algorithm (Skidmore 1990) implemented in Interactive Data Language.

Land use field data collection

The land use data for image classification and verification were collected in the field during April 2012, based on stratified random sampling. Seven strata (winter-flooded rice fields, winter-dry rice fields, rain-fed fields, open water, forest, shrub/grass, other) were identified. The size of the sample plots was 50×50 m. The geographical coordinates of the plots' centres were recorded using a GPS receiver with a positional accuracy of 5 to 10 m. Precise observation confirmation of historical land use was impossible as

the study period stretches over two decades and neither historical maps nor high-resolution images were available. Instead, historical land use of each sample plot was recorded from personal interviews with local farmers. Different actors were interviewed for the same plot to reduce potential bias. In total, 272 sample plots with constant land use throughout the study period were described and randomly divided into two equal groups for training and testing our classification.

Hybrid image classification approach

The satellite images were initially classified using a nonparametric supervised classification algorithm called Support Vector Machine (SVM). The SVM algorithm locates the optimal hyperplane decision boundary that separates classes (Brown et al. 1999). The classifier produced a land use map as well as seven rule maps each containing the probability that a pixel belonged to one of the seven classes.

A GIS-based expert system was constructed to perform post-classification sorting of the initial land use classification using additional topographic data (i.e., elevation and slope position). The expert system was described in detail by Skidmore (1989). The key mechanism of the expert system is Bayes' theorem (See Appendix for detail). The land use map and the associated probability rule maps were presented to the expert system as input. Elevation and terrain position data acted as items of evidence to infer the most probable land use type that would occur in a given grid cell. The expert system algorithm worked forward from the topographic data (item of evidence) to the hypothesis (the most probable land use type) and the search terminated only after all the evidence had been evaluated. The land use class, which had the highest posterior probability of occurring at a grid cell location, was assigned. We expected that the expert system would correct misclassifications generated by the SVM classifier.

Accuracy assessment

The accuracy of the land use map was assessed using a confusion matrix of the field observations against the classification result. The overall accuracy and Kappa coefficient (Cohen 1960) were calculated. The McNemar test for related samples (Foody 2004; De Leeuw et al. 2006) was used to evaluate the statistical significance of differences in accuracies achieved by the

classifications for 1988, 2001 and 2009, to ensure the comparability of the outputs in different time phases.

2.2.3 Change detection of winter-flooded rice fields

Post-classification comparison identified changes pixel by pixel by overlaying the three independently produced land use maps and generated the conversion matrices (1988-2001 and 2001-2009). In providing important clues to the changes, the conversion matrix can become too complicated to analyse when the number of classes being considered is high. In this study, we focused on the changes in the target class (winter-flooded rice fields).

In addition to the absolute change in area of the winter-flooded rice fields, we analysed the magnitude of the rate of change, because the same amount of habitat loss (e.g. 10%) in different areas with varied habitat availability (e.g. 10 ha versus 1000 ha) will have distinct effects on crested ibis population. Due to the different lengths of two periods, we calculated the annual rate of change as a normalized index in order to make appropriate comparisons using the compound interest rate (Puyravaud 2003) (Eq. 2.1):

$$\text{Annual rate of change} = \frac{100\%}{t_2 - t_1} \times \ln \left(\frac{A_2}{A_1} \right) \quad (2.1)$$

where A_1 and A_2 are the areas of winter-flooded rice fields at time t_1 and t_2 , respectively.

2.2.4 Prediction of population responses to the changes of winter-flooded rice fields

Population growth rate is the summary parameter of trends in population density or abundance. It can be estimated using census data since the population size of crested ibis has been measured at the same time each year. Here we interpreted the instantaneous growth rate of birth-pulse populations $r = N_{t+1}/N_t - 1$, where N_{t+1} and N_t are population sizes in the year $t+1$ and t , which was suggested by Eberhardt and Simmons (1992). We adopted the general discrete-time population model of Dennis and Otten (2000) that incorporates *a priori* models of geometric growth, logistic growth and numerical response. First, the population growth rates were regressed against population abundance to verify whether there was evidence of density dependence supporting logistic growth. The effects of population

density on population growth rate may act through their effects on food availability and associated effects on somatic growth, fecundity and survival of the species, according to a 'numerical response' (Sibly and Hone 2002). Therefore, we adopted the mechanistic paradigm and regressed the population growth rates against food availability to explain the population growth of the crested ibis. This type of numerical response was reviewed by Sibly and Hone (2002). The population's food supply is shared between its members through a process of resource competition, thus we assessed food availability by per capita availability of winter-flooded rice fields. We also verified the additive effects of population density on the instantaneous growth rate (r). Model fit was assessed firstly by statistical significance and then by the coefficient of determination (R^2). We simulated the population trends from 2001 to 2050 with the best fitted model in two scenarios that: (1) the area of winter-flooded rice fields is constant after 2009; (2) the area of winter-flooded rice fields continues to decrease/increase based on the change detection results of the present study.

2.3 Results

2.3.1 Land Use Classification

Table 2.1 Land use classification accuracy assessed by overall accuracy and Kappa coefficient. The p -value for the McNemar test greater than 0.05 indicates no significant difference between the accuracies of two compared classifications.

Classification	Overall accuracy (%)	Kappa coefficient	McNemar test		
			compared classification	χ^2	p -value
1988	89.8	0.88	2001	0.50	0.480
2001	89.3	0.87	2009	3.13	0.077
2009	90.8	0.89	1988	2.25	0.134

The classification maps for the years 1988, 2001 and 2009 in the three areas are presented in Fig. 2.3 (see Fig. A2.1 in Appendix for the maps of the whole study area). The overall map accuracies range between 89.3% and 90.8%, and the high Kappa statistics between 0.87 and 0.89, indicate the classification results are good. The McNemar test for related samples

showed no significant differences between the accuracies of the three classifications (Table 2.1), which confirmed the three classification maps were comparable for use in further analyses.

Figure 2.3 Land cover/use maps in Areas 1, 2 and 3 for the years 1988, 2001 and 2009.

2.3.2 Changes to Winter-Flooded Rice Fields

The total area covered by the winter-flooded rice fields in the whole study area decreased from 4643.19 ha in 1988 to 2806.11 ha in 2009 at an annual loss rate of 0.4% and 5.5% in the two periods, respectively. A decline in the winter-flooded rice fields was also observed from 1988 to 2009 in all three areas (Fig. 2.4). Land use types converted from and to winter-flooded rice fields in the three areas are shown in Fig. 2.5, respectively. In all three areas and two periods, very small proportions of the winter-flooded rice fields were converted to open water for human use, such as aquaculture ponds and reservoirs, that may offer an alternative habitat. Area 1 experienced different processes of land use change to winter-flooded rice fields during the two periods. From 1988 to 2001, winter-flooded rice fields in Area 1 covered more or less the same total area, with a very small net loss of less than 2 ha. However, the winter-flooded rice fields were then drastically reduced (by 47.61 ha, accounting for almost 40%) until 2009, owing to an extensive conversion to non-agricultural uses, such as shrub/grass (Fig. 2.5b). In Area 2, despite the gain of 41.40 ha in winter-flooded rice fields chiefly from winter-dry rice fields between 1988 and 2001 (Fig. 2.5a), the winter-flooded rice fields shrank from 291.15 ha to 239.67 ha during the first period with a loss rate of 1.5% per year. They continued to decline by 63.63 ha with an annual rate more than double that during the second period. Large proportions of the lost winter-flooded rice fields were converted to other arable land, accounting for 69% and 59% of the lost area in each period, respectively (Fig. 2.5b). The remainder were lost to shrub/grass or other non-agricultural uses. In Area 3, the non-protected area, a net loss of 103.68 ha and 91.53 ha of winter-flooded rice fields was observed during the two periods. The loss rate here was similar to that in Area 2 from 1988 to 2001. During the second period, the rate of loss was higher, but still lower than that seen in the core-protected areas (Fig. 2.4). The continuous reduction of winter-flooded rice fields in Area 3 was due mainly to conversion to winter-dry rice fields and rain-fed fields, which accounted for 80% and 78% of the loss in each period, respectively (Fig. 2.5b).

Figure 2.4 Change in the area of the winter-flooded rice fields in Areas 1, 2 and 3 from 1988 to 2009. The annual rate of change for each period in each area is given above the lines.

Figure 2.5 Conversions of **a.** land cover/use types to winter-flooded rice fields and **b.** winter-flooded rice fields to other land cover/use types during 1988-2001 and 2001-2009.

2.3.3 Population Dynamics in Response to the Changes of Winter-Flooded Rice Fields

There was no evidence of density dependence in the first period (i.e., before 2001) of population increase ($F = 0.07$, $p = 0.79$, $R^2 = 0.01$), whereas the population exhibited density-dependent growth in the second period (i.e., after 2001) ($F = 23.40$, $p < 0.001$, $R^2 = 0.77$). In the second period, the numerical response of the population growth rate (r) to the per capita availability of winter-flooded rice fields was highly significant ($F = 62.43$, $p < 0.001$, $R^2 = 0.87$). There was no additive effect on r of population density ($p = 0.44$), which indicates that the effect of density dependence arises through competition for food resources. The fitted regression was $r = -0.041 + 0.09 \times \ln(\text{per capita food availability})$. The regression estimates that crested ibis abundance declines when the availability of winter-flooded rice fields per ibis drops below 1.56 ha. The population trends in 50 years were simulated based on this numerical response (Fig. 2.6). In both scenarios, the population growth rate increased at first, but then declined at a faster rate. If the area of winter-flooded rice fields would stop declining, the population size increased to 1757 in 2050. In the second scenario, however, the population size approached 940 individuals at the tipping point in 2021, after which it declined due to a continuous reduction of the winter-flooded rice fields.

Figure 2.6 Numerical response of the crested ibis population to the constant amount of winter-flooded rice fields after 2009 (Scenario 1) and to the continuous reduction of winter-flooded rice fields (Scenario 2) predicting the population trends in 50 years. The cross symbol represents the tipping point in the year 2021 with the maximum population of 940.

2.4 Discussion

2.4.1 Potential impact of reduction in winter-flooded rice fields on crested ibis population

A population that is rebounding from a catastrophic decline in numbers may grow geometrically for a while when resources are abundant and predators, pathogens and competitors are absent. We found that the population of crested ibis exhibited geometric growth in the early stage of recovery, which was also confirmed by (Wang and Li 2008). In this period, the reduction of winter-flooded rice fields was relatively less and some winter-flooded rice fields were restored, especially in the core-protected areas (Fig. 2.5a). The crested ibis population behaved as if food resources were unlimited when it was small. The rapid growth of the crested ibis population and the recovery from the brink of extinction achieved through the conservation management that greatly reduced the risks of hunting,

poisoning and predation (Xi et al. 2002; Wang and Li 2008). Consequently the average survival rate of nestlings for crested ibis in the 1980s and 1990s was reported to be much higher than other endangered ibis species (Wang and Li 2008). However, we found a negative effect on the population growth rate of the reduction of winter-flooded rice fields resulting in population regulation after 2001. This relationship accounted for 87% of the variation in population growth rate, indicating the critical role of winter-flooded rice fields in the restoration of crested ibis population. The ongoing conversion of winter-flooded rice fields to dryland farming in winter or non-agricultural uses is rapidly reducing the availability of foraging habitats for the crested ibis. Food shortage has decreased the number of fledglings in some areas despite its increased breeding population size (Su 2008). The continuous reduction of winter-flooded rice fields is shown here to eventually constrain its population growth in the coming decades (Fig. 2.6). Habitat loss may further increase interspecific competition in the crested ibis and conspecific competition with other waterbirds, such as egrets. As the ibis population approaches the habitat's carrying capacity, competition will become more intense, leading to increasing death rates and decreasing birth rates, thereby threatening further restoration of the crested ibis population.

The numerical response may also be influenced by other mechanistic factors, such as the availability of suitable nesting trees, anthropogenic disturbance and pesticide exposure (Newton 1998), which may be related to the unexplained remaining variation in the population growth rate. The results reported here indicate the population change within the specific study area (Fig. 2.1). The crested ibis may emigrate from the focal study area and scatter over a wider area allowing the total population to continuously increase. Unfortunately, the fate of the emigrants is not known and due to data availability, spatial population dynamics was not considered in this study. Although it is unlikely to give exactly the same result as a model incorporating every detail, the parsimonious model described here is likely to provide useful approximations. In order to investigate density-dependent mechanisms adequately in wild populations subject to changing environmental conditions, management of endangered species, such as crested ibis, requires ongoing and quantitative assessment of trends involving demographic parameters, by following populations over time from very low population abundances to equilibrium (Sutherland and Norris 2002).

Ground truth data were assumed to be 100% accurate for the land use classification procedure, but data collection is potentially subject to bias, when no other independent sources of information (e.g., high-resolution aerial photos) are used to determine historical land use. Farmer surveys may introduce errors due to memory lapse or concern about the consequences of providing a truthful answer (Morra-Imas and Rist 2009). For instance, farmers may exaggerate the size of the winter-flooded rice fields or distort positional information in order to gain government compensation. In addition, selection bias may also exist, as farmers who volunteer participate in interviews may be systematically different from those who do not (Morra-Imas and Rist 2009). The errors in ground truth data are usually unknown and the uncertainties cannot be quantified, but they produce errors of omission (false negative) and commission (false positive) in the classification. When omission error is more than commission error, the land use category is underestimated, and vice versa (Joseph 2005). In either case, the numerical response model may be subject to the bias arising from the misclassification of the winter-flooded rice fields.

2.4.2 Causes of reduction in winter-flooded rice fields

Farmers have long been dependent on exploiting existing resources in underdeveloped, mountainous areas. Winter-flooded rice fields are created or extensively modified and maintained by humans, and they cannot be protected by completely prohibiting human use within the protected area or by restricting the type of use made of natural resources. With continuing agricultural growth and economic development, local farmers are unlikely to put a high value on winter-flooded rice fields in their own interests, due to the low yields and difficult conditions of this type of farming. According to a socio-economic survey of local communities in the distribution area of the crested ibis during 2012-2013 (Ding et al. 2013), the average annual income of 645 households was around US\$2090. Most of them derived their income from farming and egress labouring, accounting for 52.9% and 36.3% of total income, respectively. However, the average annual income from winter-flooded rice cultivation was only about US\$65 per household, thus contributing extremely little to the total income. As long as natural conditions and labour capacity permit, local farmers would rather increase their incomes by changing farming practice to crop rotations, involving higher-yield and income-generating crops on limited land (Sai et al. 2013). Consequently, the conservation management of traditional and

biodiversity-friendly farming practice is facing more obstacles and challenges.

In addition to the decline in winter-flooded rice fields across the current range of crested ibis, we found different patterns of land use conversion for the winter-flooded rice fields in the core-protected areas and non-protected areas. The rate of loss of winter-flooded rice fields in the core-protected areas was lower than or similar to that in the non-protected areas during 1988-2001. More recently, winter-flooded rice fields disappeared at a much higher rate in the protected areas. It is generally perceived that habitats in protected areas will be better protected from human activities (Liu et al. 2001; Nagendra 2008). Demographic and socio-economic pressures as well as national policies were likely responsible for the reduction of winter-flooded rice fields in the core-protected areas. As the mountain areas have been opened up and the educational level of farmers increases, more and more of the labour force and farmers in the remote mountain areas have given up their farming income and become migrant workers or self-employed to earn more money outside the poor villages (Duan et al. 2013; Sai et al. 2013). Alternatively, local residents are also being relocated from their remote mountain homes, which have been deemed unsuitable for sustaining human life, to regions with better economic prospects. This migration is a major measure to alleviate poverty and sustainably manage the ecosystem in two national policy programs, China's Western Development policy launched in 2000, and the new socialist countryside construction (Rogers and Wang 2006; Li et al. 2011). Labour migration and urbanization may reduce the use of agrochemicals and fuel wood and thereby reduce environmental stress (Duan et al. 2013), which is beneficial to the recovery of crested ibis population. However, these changes in both economic and lifestyle activities may have resulted in winter-flooded rice fields as well as other arable land being abandoned and turning into shrub/grass or waste land. In addition, China's Grain for Green Program, to return steep slopes of cultivated land to forest and grassland also contributed to the conversion of winter-flooded rice fields to shrub/grass during the second period (The program was initiated in 1999 and implemented in 2002 (Liu et al. 2008). In comparison, winter-flooded rice fields in the non-protected areas at lower elevations were exposed to more intensive disturbance due to the higher human population density and less conservation management. The lost winter-flooded rice fields were mainly

converted to winter-dry rice fields and rain-fed fields due to changes in farming practice.

Higher rates of habitat loss within protected areas is uncommon, but other cases have been found (Nagendra 2008). For instance, forest in the Monarch Butterfly Reserve in Mexico (Brower et al. 2002) and in the Wolong Giant Panda Nature Reserve in China (Liu et al. 2001) both experienced a higher rate of clearing than the surrounding areas. This was mainly attributed to uncontrolled tree felling by local communities, which resulted from pitting local economic needs against the ecological needs of wildlife. Sai et al. (2013) found that local residents were not satisfied with the current compensation for conserving the crested ibis habitat and could still easily obtain more benefits from the existing resources and thereby maximize their interests. Given the dissemination of information, the unexpected reduction of winter-flooded rice fields in protected areas hints at a conflict between conservation and local communities. Conservation efforts have to deal with a two-pronged situation: managers have few resources to invest in the protected area, and local communities live in poverty (Nagendra 2008). Such situations are common in Asia. The protection will not achieve the desired outcome simply by forcing the farmers to participate in conservation efforts, and the conflicts between conservation and local socio-economic development will be aggravated further. Maintenance and restoration of winter-flooded rice fields require the understanding and cooperation of local residents with the promotion of reforms to organic and ecological farming practices (Su 2008). Supporting or mimicking traditional agriculture is a conservation paradigm in Europe and other developed countries (Wright et al. 2012). By contrast, such agri-environmental schemes have rarely been applied in the developing world due to the more challenging social and political conditions. Legislation may need to propose incentives for biodiversity-friendly and lower-impact farming practice, thereby trying to eliminate the threats of agricultural intensification and abandonment.

Appendix

Key Mechanism of the Expert System

Let A be an item of evidence known at a given location, and let us set up a hypothesis (B_j) that the land use class j occurs at this location. The Bayes' rule can then be given as:

$$P(B_j | A) = \frac{P(A | B_j) P(B_j)}{\sum_{i=1}^n P(A | B_i) P(B_i)}; i = 1, 2, \dots, n \quad (2.2)$$

where $P(A | B_j)$ is the conditional probability that a certain grid cell location has an item of evidence (A) given B_j (see Table A2.1); $P(B_j)$ is the *prior* probability of occurrence of a land use class at a certain location that can be obtained from the rule images of the initial classification. The denominator of Eq. 2.2 is the sum of all possible cases, where n is the total number of the land use classes in this study (i.e. $n = 7$).

The expert system algorithm worked forward from the item of evidence to the hypothesis and the search terminated only after all the evidence had been evaluated. All pixels were finally relabelled by the hypothesis that possessed the highest *posterior* probability (i.e. $P(B_j | A)$).

Table A2.1 Probability rules used by the Bayesian expert system for land cover/land use mapping

Item of evidence	WD	WF	Shrub /Grass	Open water	RF	Forest	Others	
Elevation (m)	< 500	0.4	0.05	0.1	0.3	0.2	0.05	0.3
	500-600	0.3	0.2	0.15	0.2	0.5	0.1	0.15
	600-800	0.25	0.3	0.3	0.1	0.25	0.2	0.1
	800-1000	0	0.05	0.05	0.1	0.02	0.15	0.05
	1000-1300	0.08	0.08	0.02	0	0	0.3	0.05
	>1300	0	0	0.03	0	0	0.95	0
Terrain position	Gully	0.4	0.4	0	0.1	0	0.01	0.05
	Lower mid-slope	0.3	0.2	0.1	0.1	0.1	0.25	0.1
	Mid-slope	0.05	0.05	0.3	0.1	0.3	0.3	0.1
	Upper mid-slope	0.02	0	0.3	0	0.3	0.25	0.1
	Ridge	0	0	0.3	0	0.3	0.2	0.1

WD, winter-dry rice field; WF, winter-flooded rice field; RF, rain-fed field

Note: Values of zero in the table were replaced by a very small value close to zero in our calculations

Figure A2.1 Maps of the land cover/use classifications in the whole study area for 1988, 2001 and 2009

Chapter 3

Reduced Dependence of Crested Ibis on Winter-Flooded Rice Fields: Implications for Their Conservation

This chapter is based on: Sun, Y., A.K. Skidmore, T. Wang, H.A.M.J. van Gils, Q. Wang, B. Qing, and C. Ding. 2014. Reduced dependence of Crested Ibis on winter-flooded rice fields: Implications for their conservation. *PLoS ONE* 9: e98690.

3 Reduced dependence of crested ibis on winter-flooded rice fields: implications for their conservation

Abstract

The crested ibis *Nipponia nippon* was once thought to be extinct in the wild until seven birds were discovered in a remote mountain village in China in 1981. Studies suggested that winter-flooded rice fields play an essential role in nest site selection by the crested ibis and hence in their survival. Considerable efforts were therefore made to conserve the winter-flooded rice fields, but these have caused conflicts between the agricultural and conservation communities. The population and geographical range of the wild crested ibis has expanded greatly since 1981, but there is no spatial information on the winter-flooded rice fields, nor on the current association of nest sites and winter-flooded rice fields. We mapped winter-flooded rice fields across the entire current range of crested ibis using innovative remote sensing and geographical information systems (GIS) techniques. The spatial relationships between the nest site clusters and winter-flooded rice fields were quantified using Ward's hierarchical clustering method and Ripley's K-function. We show that both have significantly clumped distribution patterns and that they are positively associated. However, the dependence of crested ibis on the winter-flooded rice fields varied significantly among the nest site clusters and has decreased over the years, indicating the absence of winter-flooded rice fields is not constraining their recovery and population expansion. We therefore recommend that efforts should be made to protect the existing winter-flooded rice fields and to restore the functionality of natural and semi-natural wetlands, to encourage both *in-situ* conservation and the reintroduction of the crested ibis. In addition, we recommend that caution should be exercised when interpreting the habitat requirements of species with a narrow distribution, particularly when that interpretation is based only on their current habitat.

3.1 Introduction

Studying habitats and how species select their nest sites yields important information about animal behavioural ecology and the conservation management of endangered species (Gonzalez et al. 2008; Margalida et al. 2008; Moreno-Opo et al. 2012). Selecting a suitable nest site is critical for birds because it directly affects their reproductive success and fitness (Cody 1985). Among all the characteristics of nest sites that influence breeding success, the availability of adequate forage may be a primary force for establishing the breeding territory of many avian species (Okolelov and Shubin 2003; Barea 2012).

The rice field forms one of the main artificial wetland ecosystems in China and sustains a diverse assemblage of plant and animal species (Elphick and Oring 2003; Fritz et al. 2011; Natuhara 2013). In traditional agricultural systems, rice production involves single cropping and flooding the field while it lies fallow over a long period. The flooded rice fields provide a foraging habitat similar to natural and semi-natural wetlands for waterbirds during the winter and breeding season (Elphick 2000; Wood et al. 2010; Toral et al. 2011). In terms of conservation value, the flooded rice fields contribute considerably more to waterbird biodiversity and success than unflooded fields (Elphick and Oring 2003). Many birds benefit from this agricultural practice, including the endangered crested ibis *Nipponia nippon* (BirdLife International 2012). The crested ibis was originally widespread in East Asia, but the population declined severely during the twentieth century (Li et al. 2009). This species was thought to be extinct in the wild until seven individuals were rediscovered in a small and remote village on the southern slopes of the Qinling Mountains in China in 1981 (Fig. 3.1) (Liu 1981). Since 1981 this relict population has been carefully monitored and managed. The decline of the crested ibis was explained, in part of its distribution area, by the introduction of double cropping, i.e., replacing the winter flooding of rice fields by dryland farming of rapeseed or winter wheat, thereby reducing the foraging habitat during the winter and breeding seasons (Ding 2004; Li et al. 2009).

Figure 3.1 Map of the study area. The locations of nest sites of the Crested Ibis in 1981 and 2009 are marked.

Unfortunately, we know little about the historical breeding habitats of the crested ibis or why they selected their breeding locations, and most of the scientific research on this species has been carried out since their rediscovery. The small relict population in the Qinling Mountains had a distribution area of about 100 km². A principal component analysis by Wang, Zhao, et al. (2000) indicated one of their breeding habitat requirements was a short distance (74.1 ± 42.1 m) to winter-flooded rice fields. Li et al. (2001) used resource selection functions and found that the proximity of winter-flooded rice fields was an important factor in selecting their nest sites. A significant positive effect of winter-flooded rice fields on their selection of a nest site was confirmed by Ding (2004). As the wild population of the crested ibis continued to increase under protection, an aggregation of nest sites was observed, and these were reported to be associated with the distribution of winter-flooded rice fields (Zhang et al. 2008). In the early stage of the population recovery, almost all the researchers and conservationists interested in the crested ibis, as well as the

local authorities and local community, thought that the presence of winter-flooded rice fields would determine the survival and recovery of the wild crested ibis. Hence, the conservation policy was focused on maintaining the traditional practice of winter-flooding of rice fields and compensating the farmers for their consequent loss of income (Ding 2004). Currently, the number of nest sites has increased from the original two to over 100 (Fig. 3.2) and the distribution area of the crested ibis is 30 times larger, ranging from the mountains down to the Han River floodplain (Ding 2010). However, the winter-flooded rice fields are known to be very limited on the floodplain, based on the study of the local cropping system by Dong et al. (1992). This seemingly contradictory breeding behaviour of the crested ibis raises the question as to how the species has responded more recently to the distribution of winter-flooded rice fields, particularly because species-habitat relationships may vary over time and space (Wiens 1989; Levin 1992; Li et al. 2006).

Figure 3.2 The size of the wild population of Crested Ibis and number of nest sites from 1981 to 2009.

There are no data or analyses on the distribution and extent of winter-flooded rice fields in the current distribution range of the wild crested ibis.

Satellite-based remote sensing offers the opportunity to investigate the habitat availability for wildlife in time and space, and has been successfully applied to other bird ecology and conservation measures (Boyle et al. 2004; Senapathi et al. 2007; Toral et al. 2011). However, the temporal dynamic characteristics and the relatively narrow strips (which can be less than 30 m wide) of winter-flooded rice fields in the mountainous topography at Qinling pose challenges to traditional optical remote sensing methods. In the present study, we applied innovative remote sensing and geographic information systems (GIS) techniques to map winter-flooded rice fields, and used this information to explore the relationship between the distribution and extent of winter-flooded rice fields and the nest sites of the crested ibis over its entire range.

3.2 Methods

3.2.1 Study area and nest sites

The study area (3,980 km²) is located between 33°03' to 33°39'N and 107°10' to 107°54'E, at the intersection of the Han River plain and the southern slopes of the Qinling Mountains, China (Fig. 3.1). The elevation ranges from 370 m to 2,400 m. The crested ibis is mainly seen in the plains and middle-lower mountain regions below 1,400 m. Major land covers in the study area include forest, shrub, grass, cropland, open water, built-up areas and waste land. The cropland can be divided into rain-fed fields with dryland crop cultivation, summer-irrigated rice fields with dry fallow or rotational dryland cultivation in winter (winter-dry rice fields), and rice fields with an intentionally or naturally flooded fallow period from November to May (winter-flooded rice fields). The crested ibis forages mainly in the winter-flooded rice fields, rivers and reservoirs for frogs, loaches, eels and winkles, both in winter and spring, prior to and during the breeding season, which starts in March and lasts to June (Ding 2010).

A long-term demographic monitoring programme of the crested ibis (e.g. bird ringing and nest recording) has been carried out by the Shaanxi Crested Ibis Nature Reserve since 1981. Each year the study area is systematically searched on a weekly basis to locate nests from March to May. In the meantime, every public report of an ibis nest sites is also verified by experts from the nature reserve. The monitoring has expanded to new areas, including less accessible habitats, as the population has grown,

and we therefore believe that all the nest sites have been identified during the census and monitoring. The geographical locations of the nest sites have been recorded using a global positioning system (GPS) since 2003, and the nest sites known before 2003 were revisited in 2004 to obtain GPS coordinates. The wild population of crested ibis has increased in the last three decades, particularly in the last decade (Fig. 3.2). There were 102 nest sites in the study area in 2009, which we used to test our research questions (see Fig. 3.1 for their spatial distribution).

3.2.2 Classification of winter-flooded rice fields and associated major land cover/land use types

Preparation of satellite images and ancillary topographic data

Two cloud- and snow-free Landsat Thematic Mapper (TM) images (30 m resolution; 12 January 2009 and 5 June 2009) were selected to map the winter-flooded rice fields and associated major land cover/land use types. The TM images were geometrically rectified using 1:50,000 topographic maps and the processing utilized a second-order polynomial and nearest neighbour interpolation, resulting in a root mean square error (RMSE) of less than 0.5 pixels (15 m). All image pre-processing was executed using ENVI 4.8 (Exelis Visual Information Solutions, Colorado, USA).

Topographic information, including elevation and terrain position, was derived from 30-m ASTER Global Digital Elevation Model (DEM) Version 2, released by METI and NASA on October 17, 2011, with vertical accuracies between 10 m and 25 m RMSE (<https://lpdaac.usgs.gov/>). The DEM data were geometrically co-registered with the TM images using a second-order polynomial and nearest neighbour interpolation. Five terrain position classes – gully, lower mid-slope, mid-slope, upper mid-slope, and ridge – were calculated using the algorithm (Skidmore 1990) implemented in Interactive Data Language (IDL; Exelis Visual Information Solutions, Colorado, USA).

Land cover/land use field data collection

Permits and approvals were obtained from Shaanxi Hanzhong Crested Ibis National Nature Reserve for this study, including the fieldwork within the reserve. Fieldwork did not involve any endangered or protected species.

The land cover/land use data for image classification and verification were collected in the field during April 2012, based on stratified random sampling. Seven strata (winter-flooded rice fields, winter-dry rice fields, rain-fed fields, open water, forest, shrub/grass, and other) were identified. The size of the sample plots was 50×50 m. The geographical coordinates of the plots' centres were recorded using a GPS receiver with a positional accuracy of 5–10 m. In total, we described 768 sample plots and randomly divided them into two equal groups for training and testing the classification.

Hybrid image classification approach

The satellite images were initially classified using a nonparametric supervised classification algorithm, called Support Vector Machine (SVM). The SVM algorithm locates the optimal hyperplane decision boundary that separates classes (Brown et al. 1999). The classifier produced a land cover/land use map as well as seven rule maps in ENVI 4.8. Each rule map contained the probability that a pixel belonged to one of the seven classes.

A GIS-based expert system was constructed to perform post-classification sorting of the initial land cover/land use classification using additional topographic data (i.e., elevation and terrain position). The expert system was described in detail by Skidmore (1989). The land cover/land use map and the associated probability rule images were presented to the expert system as input. Elevation and terrain position data acted as items of evidence to infer the most probable land cover/land use type that would occur in a given grid cell. The key mechanism of the expert system is Bayes' theorem. Let A be an item of evidence known at a given location, and let us set up a hypothesis (B_j) that the land cover/land use class j occurs at this location. The Bayes' rule can then be given as:

$$P(B_j | A) = \frac{P(A | B_j)P(B_j)}{\sum_{i=1}^n P(A | B_i)P(B_i)}; \quad i = 1, 2, \dots, n \quad (3.1)$$

where $P(A | B_j)$ is the conditional probability that a certain grid cell location has an item of evidence (A) given B_j (see Table A3.1 in Appendix); $P(B_j)$ is the *prior* probability of occurrence of a land cover/land use class at a certain location that can be obtained from the rule images of the initial classification.

The denominator of Eq. 3.1 is the sum of all possible cases where n is the total number of the land cover/land use classes in this study (i.e. $n = 7$).

The expert system algorithm worked forward from the item of evidence to the hypothesis and the search terminated only after all the evidence had been evaluated. All pixels were finally relabelled by the hypothesis that possessed the highest *posterior* probability (i.e. $P(B_j|A)$). We expected the expert system would correct misclassifications generated by the SVM classifier. The expert system algorithm was programmed in C# with Microsoft .NET framework.

Figure 3.3 Land cover/land use map generated by the hybrid classifier. The inset shows a zoomed-in map of a specific sample area.

The accuracy of the land cover/land use map was assessed using a confusion matrix of the field observations ($n = 384$) against the classification result. The overall accuracy and Kappa statistic (Cohen 1960) were both improved by the expert system (see Table A3.2 in Appendix). The McNemar test for related samples (Foody 2004; De Leeuw et al. 2006) confirmed the superiority of the hybrid classifier ($\chi^2 = 34.03$, $p < 0.001$). The class of winter-flooded rice fields achieved a producer's and user's accuracy of 89.3% and 90.4%, respectively. The final map of all land cover/land use types is presented in Fig. 3.3.

3.2.3 Spatial statistical analyses

To investigate the spatial variation of winter-flooded rice field habitats, we quantified the abundance of such fields around nest sites. The average foraging distances of breeding crested ibis were observed to be at least 0.56 ± 0.68 km and at most 2.82 ± 1.69 km at different periods of the breeding season (Liu et al. 2003). We therefore assumed a conservative radius of 3 km for buffers around the nest sites. The area of winter-flooded rice fields within the 3-km buffer around each nest was calculated using Spatial Analyst Tools in ArcGIS 10.0. The extent of the winter-flooded rice fields was distinguished using Ward's method (Ward 1963), constrained *a priori* to three levels (i.e., high, medium and low) (see Fig. A3.1 in Appendix). Ward's method is one of the most widely used hierarchical cluster analysis algorithms, and it has the advantage that it can select the optimal number of clusters and create clusters with a high degree of uniformity (Guillen et al. 2004; Dillner et al. 2005). Ward's method was also used to identify nest site clusters based on their geographical locations. The differences in the area of winter-flooded rice fields within the 3-km buffers around the nests were compared among the nest site clusters using the Kruskal-Wallis test followed by a pairwise Mann-Whitney U test.

Ripley's K-function (Ripley 1976) was used to further examine the spatial patterns of nest sites and winter-flooded rice fields, and to test whether the spatial distribution of the fields correlated with nest locations for all the sites together, as well as for each nest site cluster. The K-function is a tool for quantification of spatial pattern intensity of completely mapped point data (i.e., locations of all the nest sites or winter-flooded rice fields in a predefined study area), by utilizing a random species distribution over a range of distances (Ripley 1976; Dixon 2002). It compares the number of points within any distance to an expected number for a spatially random

distribution. The classification data of the winter-flooded rice fields were converted from raster data to point features using the Conversion Tool in ArcGIS 10.0 (ESRI, Inc., Redlands, California, USA). We used the L-function, the linearized form of the K-function, to aid in interpretation and to stabilize the variance (Besag 1977; Dixon 2002). Under the null model of complete spatial randomness (CSR), the theoretical value of the L-function is 0, whereas a positive value indicates a clumped distribution and a negative value indicates a regular distribution at a specific distance. The edge correction was superfluous because no nests were located outside the study area. The bivariate and multivariate generalizations of the K-function and L-function characterize the spatial associations between two or more variables (Dixon 2002; Fortin et al. 2002). The population independence hypothesis assumes that the location of points of a given population (i.e. nest sites or winter-flooded rice fields) is independent of the location of points of the other (Goreaud and Pelissier 2003). We therefore tested the bivariate L-function against the null hypothesis of population independence to determine the spatial relationship between the nest sites and winter-flooded rice fields. Theoretically, the L-function is positive if the two populations of points are positively associated and negative if they are negatively associated.

We used Monte Carlo simulations to generate 95% confidence envelopes for the L-function under the null hypothesis from 1,000 random permutations. If the observed L-function lies above the upper envelope (or below the lower envelope), the null hypothesis can be rejected. For the univariate L-function, positive differences between the observed L-function and the upper envelope of the null hypothesis of CSR indicate that the points are more clumped than expected by chance. Similarly, negative differences between the observed L-function and the lower envelope of the null hypothesis of CSR indicate that the points are more regular than expected by chance. For the bivariate L-function, positive differences between the observed L-function and the upper envelope of the null hypothesis of population independence indicate a spatial attraction between the two populations of points. Similarly, negative differences between the observed L-function and the lower envelope of the null hypothesis of population independence indicate a spatial repulsion between the two populations of points.

The univariate K-function and L-function were computed at 500 m intervals and using distances of 500 m to 30,000 m (i.e. half of the smallest edge

length of the study area was taken as the largest distance for analysis set by the software package). The bivariate functions were calculated at 500 m intervals using distances of 500 m to 3,000 m based on the foraging distance range. All the calculations and simulations were computed using the R statistical package 'ads' (spatial point patterns analysis) (Pelissier and Goreaud 2010). In addition, the estimated L-functions were compared using Analysis of Variance (ANOVA) to confirm the differences in the spatial associations between nest sites and winter-flooded rice fields among the nest site clusters. Post-hoc pairwise comparisons were performed using Tukey's Honestly Significant Difference (HSD) test.

3.3 Results

3.3.1 Spatial patterns and associations of nest sites and winter-flooded rice fields

The values of the L-functions for the distributions of both nest sites and winter-flooded rice fields differed from zero and were above the upper bound of the 95% confidence interval at all distances from 500 m to 30,000 m (Fig. 3.4), which led us to reject the null hypothesis of random distribution. These results indicate that the nest sites and winter-flooded rice fields were clumped, irrespective of distance. We also rejected the null hypothesis of population independence based on the bivariate L-function analysis, as the observed results lay outside the confidence envelope. A significant positive spatial association between the nest sites and winter-flooded rice fields was apparent at all distances from 500 m to 30,000 m (Fig. 3.5).

Figure 3.4 Plot of univariate L-function against distance r showing the spatial pattern. **A.** Distribution of nest sites. **B.** Distribution of winter-flooded rice fields. Solid lines are observed values of $L(r)$. Dotted and dashed lines are the theoretical values and the 95% confidence envelopes, respectively, for the pattern expected from a random distribution. Values of $L(r)$ above the upper envelope indicate a significantly clumped distribution at distance r . Values of $L(r)$ below the lower envelope indicate a significantly regular distribution at distance r .

Figure 3.5 Plot of bivariate L-function for the spatial association between nest sites and winter-flooded rice fields. Solid lines are observed values of $L_{12}(r)$. Dotted and dashed lines are the theoretical values and the 95% confidence envelopes, respectively, for the pattern expected under the null hypothesis of population independence. Values of $L_{12}(r)$ above the upper envelope indicate a significant positive association, whereas values of $L_{12}(r)$ below the lower envelope indicate a significant negative association.

3.3.2 Nest site clusters and their association with winter-flooded rice fields

We distinguished five clusters of nest sites: Clusters A, B and C were on the southern slopes of the Qinling Mountains, Cluster D was to the south of the Han River, and Cluster E was on the floodplain. The extent of winter-flooded rice fields around the nest sites varied significantly among these five clusters (Kruskal-Wallis $\chi^2 = 59.05$, $p < 0.001$) (Figs. 3.6 and 3.7). The nests of Cluster E extended over the smallest area of the winter-flooded rice fields (4.13 ± 2.29 ha), while Clusters B and C had a much greater extent (70.07 ± 20.34 ha and 51.79 ± 23.06 ha, respectively). Clusters A and D covered an intermediate area size (26.95 ± 17.87 ha and 24.24 ± 8.77 ha, respectively) and were not significantly different from each other (Fig. 3.7).

Figure 3.6 Nest site clusters and the extent of winter-flooded rice fields. Five clusters (A-E) were identified based on their geographical locations, using Ward's hierarchical clustering method. They are shown in different colours. The extent of winter-flooded rice fields within 3-km buffers around the nest sites are delineated by circles of three different sizes (high, medium and low). The locality name and year when the first nest site was established in each cluster are given above and below the line, with the total number of nests per cluster in parentheses.

Figure 3.7 Differences in the area of winter-flooded rice fields in the nest site clusters. The area of winter-flooded rice fields within 3-km buffers around the nest sites in the five clusters (A-E) is shown by box plots. The only pair with no significant difference is annotated based on pairwise Mann-Whitney U tests ($p \geq 0.05$).

The bivariate L-function analyses showed that the spatial association between the nest sites and winter-flooded rice fields varied for the five nest site clusters (Fig. 3.8). Cluster A showed a significant positive dependence on winter-flooded rice fields at distances of 500 m to 1,500 m. The positive dependence for Cluster B was marginally significant up to about 2,000 m, but significant at larger distances. For Cluster C, the spatial aggregation between nest sites and winter-flooded rice fields appeared to be significant at distances of 500 m to 1,000 m. In contrast, the bivariate L-function analysis failed to detect any significant spatial associations in Cluster D at all distances from 500 m to 3,000 m (Fig. 3.8D). The nest sites in Cluster E

are spatially independent of winter-flooded rice fields up to 1,500 m, although a segregation was detected at distances of 1,500 m to 2,500 m (Fig. 3.8E). The result of one-way ANOVA confirmed the significance of differences in these spatial associations among the five nest site clusters ($F = 45.62$, $p < 0.001$). The post-hoc test found the difference between each pair of means was significant at an alpha level of 0.05, except for the pair of Clusters B and C, which were established in the same year (2001) (Fig. 3.9).

Figure 3.8 Spatial association between nest sites and winter-flooded rice fields in the nest site clusters. Bivariate L-function $L_{12}(r)$ against distance r for each cluster is plotted (A-E). Solid lines are observed values of $L_{12}(r)$. Dotted and dashed lines are the theoretical values and the 95% confidence envelopes, respectively, for the pattern expected under the null hypothesis of population independence. Values of $L_{12}(r)$ above the upper envelope indicate a significant positive association, whereas values of $L_{12}(r)$ below the lower envelope indicate a significant negative association. The year when the nest site was first established in the cluster is given.

Figure 3.9 Variations in the spatial association between nest sites and winter-flooded rice fields over the years. Observed L-function values from bivariate L-function analysis for the five nest site clusters (A-E) established over the years are shown by box plots. The only pair with no significant difference is annotated based on post-hoc pairwise Tukey's HSD test ($p \geq 0.05$).

3.4 Discussion

Our study shows that the nest sites of crested ibis and winter-flooded rice fields exhibit a significantly clumped distribution pattern. The nest sites are positively associated with the winter-flooded rice fields over the birds' entire distribution range. This association suggests that the clumping of the nest sites may be a response to the distribution of the winter-flooded rice fields (which can be patchy). Our results agree with the findings that birds' nests are spatially clumped in response to the heterogeneity in their available resources (Kiestler and Slatkin 1974; Cornulier and Bretagnolle 2006; Johnson and Walters 2011). Other studies in the small relict crested

ibis population (NW portion of Cluster A) focused on sample plots and showed that the winter-flooded rice fields had a significant effect on where the birds chose to nest (Wang, Zhao, et al. 2000; Li et al. 2001; Ding 2004). Yu et al. (2010) described how all the natal home ranges were close to winter-flooded rice fields with regard to the postfledging and natal dispersal of the crested ibis. Our findings are based on a spatial analysis of the entire population in 2009 and confirm the positive association between winter-flooded rice fields and nest sites during the recent expansion of the crested ibis's range.

We observed and confirmed variations in the spatial associations between the nest sites and winter-flooded rice fields among the nest site clusters (Figs. 3.8 and 3.9). A spatial attraction (i.e., positive association) was found in Clusters A, B and C. The larger area of winter-flooded rice fields in Clusters B and C may increase the birds' food searching efficiency and reduce their energy consumption, which could, in turn, increase their reproductive fitness (Macarthur and Pianka 1966; Yu et al. 2006). Spatial dependencies were seen at different distances in Clusters A-C, suggesting that the distribution of winter-flooded rice fields is not the only habitat factor that has an effect on where the crested ibis choose to nest. The presence of suitable nesting trees, as well as human disturbances (e.g., hunting and mining), also limits the distribution of the breeding crested ibis (Wang, Zhao, et al. 2000; Li et al. 2001; Ding 2004; Li et al. 2006). We noted that Cluster B showed a stronger dependence on the winter-flooded rice fields and was at a greater distance than Clusters A and C (Fig. 3.8A-C). A plausible explanation seems to be that the larger patches of rice fields indicate more intensive human activities at lower elevations in Cluster B, where several strips of winter-flooded rice fields are near busy roads (observed during the fieldwork). The relatively high disturbance from the roads may constrain the establishment of nesting crested ibis compared to Cluster C, where there were more forest areas at higher elevations. However, Cluster A had a smaller extent of winter-flooded rice fields, but there were dozens of nest sites established here and they formed the largest cluster (Fig. 3.6). Besides the habitat factor, the crested ibis' social behaviour, e.g. conspecific attraction, may also be responsible for its pattern of nest site selection (Stamps 1988; Melles et al. 2009). However, we would expect fewer new nest sites to be established in this area in the future, since the specific foraging resources are limited and the birds' dependence on these resources is strong.

The preference of the crested ibis for winter-flooded rice fields is, however, no longer apparent after their expansion out from the relict population. Nest sites have been found to the south of the Han River (Cluster D) and on the floodplain (Cluster E) since 2002 and 2004, respectively, where the extent of winter-flooded rice fields is low to scarce. These two most recently established clusters are at a low elevation, and the crested ibis has shown no preference for nesting near winter-flooded rice fields (Fig. 3.8D-E). Wetlands at low elevations, such as riverbanks, reservoirs and rice field channels, can act as alternative winter habitats and also provide the crested ibis with abundant food (Zhai et al. 2001; Wang and Li 2008; Maltchik et al. 2011). Despite the different dependencies seen for winter-flooded rice fields in their selection of nest sites, no significant variation in the number of successful nests and their breeding success at different altitudes was found (Yu et al. 2006). Wang and Li (2008) pointed out that the fledging success of the crested ibis did not differ between low- and high-elevation habitats. They also indicated that the low-elevation habitats, with a limited extent of winter-flooded rice fields, were capable of sustaining the crested ibis population inhabiting the area by offering the birds alternative foraging habitats. From a conservation point of view, the breeding success in relation to future habitat shifts should be investigated.

Intensive human disturbance (e.g., changing farming practices) and the high risk of human-induced mortality (due to hunting and use of toxic pesticides) historically led to a reduction in the crested ibis population at low elevations (Ding 2010) and displaced them to more remote and higher montane areas where there was a lower human impact and consequently less risk (BirdLife International 2001; Wang and Li 2008; Li et al. 2009). The optimal habitats for survival and reproduction may remain unoccupied or under-utilised locally, depending on the proximity of alternative habitats with less disturbance (Lopez-Jamar et al. 2011). Habitat use and selection change may indicate changing population constraints, such as less hunting pressure or less exposure to toxic pesticides in the floodplain area due to decades of conservation efforts. The rapid increase in the crested ibis population, with the observed shift in nesting habitats, suggests that these birds might have previously been restricted to suboptimal mountainous habitats at high elevations in the past (Wang and Li 2008). The recently expanding population could be showing a return to more varied habitats. Furthermore, the changing role of winter-flooded rice fields in choosing where to nest may also suggest the crested ibis can show behavioural

plasticity and an adaptive response to a heterogeneous environment. The behavioural plasticity in habitat selection and an ability to adapt to habitat heterogeneity may allow the birds to balance limitations experienced in the available habitats (Treinys et al. 2008; Jia et al. 2013). Other waders, such as Terek Sandpipers *Xenus cinereus*, of which nests have been found in a wide range of habitats, also show behavioural plasticity in adapting to different environmental conditions, including urban areas (Meissner et al. 2012). Another example is the range expansion and adaptation to increased human activity reported for the Black Stork, *Ciconia nigra* (Treinys et al. 2008). Similarly, the recovering Spanish Imperial Eagle, *Aquila adalberti*, population has returned from its less populated habitats to the human-occupied plains it formerly favoured, now that it is legally protected and its habitats are sympathetically managed (Gonzalez et al. 2008).

3.4.1 Conservation implications

Our findings have important implications for the management and recovery planning of endangered species in general, and for crested ibis conservation, in particular. Firstly, natural wetlands have been decreasing globally and waterbirds have become increasingly dependent on rice agriculture for their survival (Donald 2004). Traditional rice production provided essential habitats for the survival and reproduction of crested ibis during the early stage of the relict population recovery, and still has a positive influence on their conservation. It is advocated that some patches of winter-flooded rice fields should be uniformly maintained especially in the area with less natural and semi-natural wetland, otherwise the crested ibis will find it difficult to survive. The conflicting interests of farmers and the crested ibis in these areas still need to be resolved by financial compensation.

Secondly, our study provides a better understanding of the contribution that traditional rice production can make to the reintroduction of the crested ibis. Although the population of crested ibis is now increasing in size and expanding its range, its current distribution range is still too limited for it to be confronted with the risks of natural catastrophes, such as disease. Efforts to reduce their risk of extinction have been carefully prioritised for potential reintroductions (Yu et al. 2006; Ding 2010). We show that the dependence of the crested ibis on this specific habitat varies over space and that it has decreased over the years with the growth and expansion of the wild population. Our finding provides some guidance on the selection of reintroduction sites and indicates that the absence of winter-flooded rice

fields is not a constraint to the recovery and expansion of the population. The conservation effort of widely encouraging rice cultivation practices that involve single cropping and extended periods of fallow flooding (BirdLife International 2012) may thus only be partially effective. We therefore recommend that an effort should be made to actively protect the existing winter-flooded rice fields, and to restore the functionality of natural and semi-natural wetlands for both the *in-situ* conservation and reintroduction of the crested ibis. Apart from the crested ibis, the knowledge of the historical habitat selection factors of many endangered species is limited. Our study supports the view that caution should be exercised when interpreting the habitat requirements of species whose distribution is restricted to just one or a few localities, particularly when that interpretation is based only on current habitats (Gonzalez et al. 2008; Wang and Li 2008).

Thirdly, we show that the investigation and monitoring of wildlife habitats using innovative remote sensing and GIS techniques can increase understanding of species-habitat relationships and can provide timely and accurate information for conservation and management decisions. This is particularly true when it comes to large areas with difficult access. In this study, we have demonstrated satellite images are effective for mapping winter-flooded rice fields across the study area. These spatially continuous, streams of habitat data are not, however, likely to be collected by ground surveys alone. Distinguishing man-made habitats from natural and semi-natural habitats may be challenging but it is very important, as the implications for management will vary greatly depending on the types of habitats and how they are created or maintained.

Appendix

Figure A3.1 Three levels of the extent of winter-flooded rice fields. The area of winter-flooded rice fields within 3-km buffers around the nest sites was categorized into high-, medium- and low levels using Ward's hierarchical clustering method.

Table A3.1 Probability rules used by the Bayesian expert system for land cover/land use mapping

Item of evidence	WD	WF	Shrub /Grass	Open water	RF	Forest	Others	
Elevation (m)	< 500	0.4	0.05	0.1	0.3	0.2	0.05	0.3
	500-600	0.3	0.2	0.15	0.2	0.5	0.1	0.15
	600-800	0.25	0.3	0.3	0.1	0.25	0.2	0.1
	800-1000	0	0.05	0.05	0.1	0.02	0.15	0.05
	1000-1300	0.08	0.08	0.02	0	0	0.3	0.05
	>1300	0	0	0.03	0	0	0.95	0
Terrain position	Gully	0.4	0.4	0	0.1	0	0.01	0.05
	Lower mid-slope	0.3	0.2	0.1	0.1	0.1	0.25	0.1
	Mid-slope	0.05	0.05	0.3	0.1	0.3	0.3	0.1
	Upper mid-slope	0.02	0	0.3	0	0.3	0.25	0.1
	Ridge	0	0	0.3	0	0.3	0.2	0.1

WD, winter-dry rice field; WF, winter-flooded rice field; RF, rain-fed field

Note: Values of zero in the table were replaced by a very small value close to zero in our calculations

Table A3.2 Classification accuracy produced by the support vector machine (SVM) classifier and the integrated SVM and GIS expert system (hybrid classifier).

Class	SVM classifier		Hybrid classifier	
	Prod. Acc.(%)	User Acc.(%)	Prod. Acc.(%)	User Acc.(%)
Winter-dry rice field	80.0	81.6	92.0	90.2
Winter-flooded rice field	88.1	71.8	89.3	90.4
Shrub/Grass	70.0	77.8	77.5	96.9
Open water	86.0	100.0	98.0	100.0
Rain-fed field	76.0	82.6	92.0	85.2
Forest	75.0	83.3	91.7	84.6
Others	90.0	84.9	94.0	94.0
Overall accuracy (%)	81.5		90.8	
Kappa	0.78		0.89	

Chapter 4

Predicting and Understanding Spatio-Temporal Dynamics of Species Recovery: Implications for Crested Ibis Conservation in China

This chapter is based on: Sun, Y., T. Wang, A.K. Skidmore, S.C.F. Palmer, X. Ye, C. Ding, and Q. Wang. 2016. Predicting and understanding spatio-temporal dynamics of species recovery: implications for Asian crested ibis *Nipponia nippon* conservation in china. *Diversity and Distributions* (in press).

4 Predicting and understanding spatio-temporal dynamics of species recovery: implications for crested ibis conservation in china

Abstract

Some threatened species are now recovering after a period of serious decline. Understanding and predicting the spatio-temporal recolonization of these species in a heterogeneous landscape are important for their conservation planning. We aimed to predict the range expansion of the endangered Asian crested ibis (*Nipponia nippon*) as it recovers from near-extinction in order to guide its *in-situ* conservation and plan possible reintroductions. We used a presence-only ecological niche model to predict breeding habitat suitability and a newly developed, spatially explicit and individual-based dynamic modelling platform to simulate range expansion. We performed a sensitivity analysis to assess the effects of uncertainty in demographic and dispersal parameters on the simulation of range dynamics. The impact of human-induced mortality risk was also investigated. Predictions showed that the Asian crested ibis population and the range extent would continue to increase over the next 50 years, and the species would recolonize parts of its historical range. However, the majority of the population would still be restricted to a relatively small region, and some potential suitable regions might not be recolonized for decades by natural dispersal. Moreover, the simulated range dynamics were sensitive to life-history trait parameters, among which adult survival probability and the proportion of long-distance dispersal events showed the strongest effects. High human-induced mortality risks had a significant negative effect on population growth and range expansion. This study demonstrates how hybrid modelling can inform conservation management of threatened species as they recolonize former habitat. The findings enable prioritization of management efforts, highlight the need for long-term monitoring of the key life-history parameters, and provide evidence to guide the selection of potential reintroduction sites for the long-term survival and recovery of target species.

4.1 Introduction

Many bird species have become regionally extinct, or their populations seriously reduced, owing to habitat loss and degradation, human persecution and hunting (Suckling et al. 2012; Deinet et al. 2013). Conservation efforts focused on legal protection, habitat management and restoration, as well as species reintroductions, have increased populations and the recolonization of former range for a number of species, such as the white stork *Ciconia ciconia* and Dalmatian pelican *Pelecanus crispus* in Europe (Deinet et al. 2013) and the Aleutian cackling goose *Branta hutchinsii leucopareia* in North America (Suckling et al. 2012). The population increase and range expansion of threatened but recovering species, can nevertheless pose challenges for their conservation, especially from conflict with humans (Ding 2004; Marucco and McIntire 2010). The accurate prediction of potential habitat and species range dynamics is therefore imperative to plan the recovery of target species.

Historically, crested ibis *Nipponia nippon* was widely distributed and commonly reported. It used to nest in the Russian Far East, Japan, and mainland China, and was presumed to be a non-breeding visitor to the Korean peninsula and Taiwan, but it is now extinct over almost all of its former range (BirdLife International 2016). The single relict population of seven birds surviving in the wild was found in 1981 in the Qinling Mountains in Shaanxi province, China (Liu 1981). The dramatic decline of the species during the mid-twentieth century has been attributed to the combined influence of habitat loss (due to changing farming practices) and the high risk of human-induced mortality (due to hunting and use of toxic pesticides) (Li et al. 2009; Ding 2010). Coupled with continued and strong legal protection, numerous conservation measures have been undertaken, including nest guarding, prohibiting hunting and logging, raising public awareness, stakeholder dialogue (involvement in active conservation) and habitat management (e.g., agri-environmental schemes) (Xi et al. 2002). Such measures have all contributed to on-going recovery of the crested ibis, such as the higher breeding success compared with many other nidicolous birds (Yu et al. 2006). Currently, the number of nest sites has increased from the original two to over 100, and the geographical range has been expanded 30-fold (Ding 2010). Following the successes of captive breeding programmes, captive bred birds are now being used to reintroduce the species to parts of its former range in China and Japan (Yamagishi 2009; Yu et al. 2009).

However, the crested ibis remains endangered (BirdLife International 2016); the majority of the wild population is restricted to the original small range and its future status is uncertain. In this context, the range dynamics of the wild crested ibis has interested conservation biologists, based on their desire to identify where this species will be in the future.

Range expansion is a highly dynamic process, not only determined by the interplay of demographic and dispersal phenomena, but also by biotic interactions and abiotic landscape influences, such as habitat availability and fragmentation (Hastings et al. 2005; Kubisch et al. 2014). Many researchers have advocated adopting hybrid modelling approaches for species range expansion that couple correlative, phenomenological species distribution models (SDMs) with mechanistic models of population dynamics (Wintle et al. 2005; Franklin 2010; Gallien et al. 2010). Hybrid models have been used to explore the impacts of environmental change on species since the development of RAMAS GIS in the 1990s (Akçakaya 1994). There has been considerable progress towards such integration of modelling approaches, including application to the expansion dynamics of biological invasions (Fraser et al. 2015) and species recovery (Marucco and McIntire 2010), impacts of global change on species distributions and persistence (Keith et al. 2008; Zurell et al. 2012; Naujokaitis-Lewis et al. 2013) and evaluation of land management and conservation options (Akçakaya et al. 2004; Wintle et al. 2005; Southwell et al. 2008). The common method of hybridisation is to constrain the basic demographic parameters of the dynamic model (e.g., carrying capacity, survival or fecundity) by habitat suitability derived from SDMs (Gallien et al. 2010).

An individual-based modelling (IBM) approach has recently been increasingly used for dynamic modelling of species populations (Zurell et al. 2012; Aben et al. 2014; Heikkinen et al. 2014; Fraser et al. 2015). An IBM can incorporate individual variability, and allow for stochastic demographic effects and explicit simulation of animal movement across realistic landscapes (Aben et al. 2014; Greta Bocedi et al. 2014). However, hybrid models of habitat suitability and spatially explicit population dynamics are only feasible and informative if the life-history parameters and habitat requirements of the species are well understood. Model outputs can be sensitive to uncertainty in estimates of species' dispersal abilities and demographic parameters (Zurell et al. 2012; Heikkinen et al. 2014). These uncertainties need to be quantified in order to draw inferences about the robustness of model results. On the other hand, conservation management

may also benefit from understanding the impacts of uncertainties in parameterisation, and which parameters, especially those controllable or affected by management actions, have greater influences on species range dynamics (Marcot et al. 2015).

The main objective of this study was to understand and predict the natural breeding-range expansion process of the wild crested ibis in a heterogeneous but relatively stable landscape during the next 50 years. To achieve this, we firstly used a presence-only ecological niche model to predict current breeding habitat suitability in central China, and secondly an IBM to link this species-environment relationship to population dynamics and simulation of range expansion. We performed a sensitivity analysis to evaluate the variability in range dynamics introduced by the uncertainty in demographic parameters and the dispersal ability of the species.

4.2 Methods

4.2.1 Study area and species data

The wild population of crested ibis is currently distributed during the breeding season within the range between 32°53′ to 33°43′N and 107°3′ to 107°55′E, at an elevation of up to 1200 m. The current range is mainly located on the southern slopes of the Qinling Mountains and on the Han River plain in Shaanxi province, China. Our study area (1,538,600 km²) is centred around the current range of crested ibis up to a radius of 700 km, which incorporates parts of several adjacent provinces (Fig. 4.1). We chose this area to cover sufficiently the potential range expansion during the next 50 years, and to facilitate the identification of potential suitable habitat. We refer to the current breeding range of crested ibis as the local range, and the 700 km radius around the local range as the whole study area.

Figure 4.1 Map of the study area and the current range (local range) of breeding crested ibis in China. The locations of nest sites in 2011 are marked with black dots.

Monogamous crested ibis breeds once a year starting in late February to early March. It nests and roosts in tall trees near to wetlands or agricultural land which provides forage (Sun et al. 2014). The population is resident, but exhibits local seasonal movement during summer and winter. Juveniles leave the natal home range after they become independent of their parents, and move to wintering areas. The mean natal dispersal distance of females (9.6 km) exceeds that of males (5.9 km) (Yu et al. 2010). The young birds are sexually mature in 2-3 years, but occasionally start breeding at 4-7 years of age (Ding 2010; Yu et al. 2010). Breeding pairs tend to reuse the same nest sites in subsequent years subject to no disturbance (Ding 2004). A long-term monitoring programme for ringing crested ibis and recording nest locations has been carried out by government and the local conservation agency. Each year the core protected area of the breeding range is systematically searched to locate nests from March to May, supplemented by verification of nest locations reported by the public in surrounding areas and neighbouring counties. We obtained the geographical coordinates of nest site locations from 1994 to 2011 from Shaanxi Hanzhong Crested Ibis National Nature Reserve, and used the records in 1994 ($n=6$) and 2011

(n=123) as species occurrence data in the models, having first removed duplicate presence records in the same grid cell (total n=100).

4.2.2 Habitat suitability modelling

Remote sensing has produced geospatial datasets and analytical algorithms for mapping biogeographical heterogeneity. Satellite-derived vegetation and water indices are indicative of favourable habitats and feeding areas for waterbirds and have been used in ecological modelling of their spatial distributions (Cappelle et al. 2010). In this study, we used the Normalized Difference Vegetation Index (NDVI) and Land Surface Water Index (LSWI) as environmental predictors to model habitat suitability for breeding crested ibis. Additional predictors included in the model comprised lidar-derived canopy height, bioclimatic variables, elevation and human population density. All spatial data were resampled to 1 km resolution (see Appendix and Table A4.1).

The habitat suitability model was developed using the maximum entropy model, MaxEnt v3.3.3k, a machine learning algorithm for predicting species distribution and habitat suitability from presence-only data and environmental variables (Phillips et al. 2006). MaxEnt can handle complex interactions between response and predictor variables (Elith et al. 2006; Elith et al. 2011), and is insensitive to small sample sizes (Wisz et al. 2008). It has been found to be stable with respect to correlated variables (Elith et al. 2011), and therefore all the environmental predictors were retained, as all were potentially ecologically relevant. It has been shown that if species occurrences are restricted to a fraction of the study area, model performance can be enhanced by drawing background points from this fraction of the area, and the reliability of the prediction should be improved when the model is extrapolated to the whole study area (Phillips 2008; Phillips et al. 2009). Thus, 500 background points were randomly selected within the local range, which was sufficient for a good representation of all environments in such a limited spatial extent. Our MaxEnt model was run with the recommended default settings for features and regularization. Ten replicates were run, and for each replicate, 70% of nest site localities (n=70) were randomly selected for model training and the remaining 30% withheld for testing (n=30). The default output of MaxEnt is a continuous variable ranging from 0 to 1, where high values indicate higher relative suitability. The accuracy of the model prediction was evaluated by the area under the receiver operating characteristic curve (AUC) and the true skill statistic

(TSS) (see Appendix for details). A built-in jackknife test was executed with each run of MaxEnt model, allowing the estimation of the relative importance of environmental variables in computing the habitat suitability.

4.2.3 Range expansion modelling

Range expansion modelling was conducted using RangeShifter v1.1, a platform for spatially explicit, individual-based modelling of species range dynamics (Greta Bocedi et al. 2014), which integrates population dynamics and dispersal models. The cell-based model ran over the habitat suitability map reprocessed for range expansion modelling (see Appendix for detail). We assumed constant habitat suitability during the simulation period and a linear relationship between habitat suitability and carrying capacity.

Population dynamics

Many bird populations are modelled with males only because they establish territories, and therefore, limit population growth (McCarthy et al. 2004; Wakamiya and Roy 2009). Additionally, males were found to be the philopatric sex in crested ibis (Liu 2013) and on average disperse shorter distances than females (Yu et al. 2010). We therefore implemented a male-only model, and we assumed that males determined the spatial population dynamics and could always find a mate. We used a stage-structured population model, which required a transition matrix based on a Leslie matrix (Greta Bocedi et al. 2014). The model included three stage classes: juveniles (<1 yr), subadults (1-2 yrs) and adults (≥ 2 yrs). In RangeShifter, juvenile non-dispersal mortality was included in fecundity constrained by density dependence. Only adults had a nonzero fecundity rate, and survival estimates were stage specific. We assumed all surviving subadults would develop to adults after age 2 at low density (i.e., in the absence of competition) in a high suitability cell. We then applied the following transition matrix:

$$\begin{bmatrix} 0 & 0 & \Phi \\ 1.0 & 0 & 0 \\ 0 & Ss & Sa \end{bmatrix}$$

where Ss is subadult survival probability, Sa is adult survival probability, and $\Phi=2$, which represents two male offspring per male on average at low density in a high suitability cell, assuming a 1:1 sex ratio.

We assumed every reproductively mature male would reproduce every year. The crested ibis is able to reproduce up to a maximum age of 16 (Yu et al. 2007), and individuals growing older than 16 were removed from the simulation. Demographic stochasticity was included via a Poisson distribution, from which a discrete number of offspring produced by each reproductive individual was generated. We assumed that density dependence would act on both reproduction and development, which was implemented as an exponential decay in RangeShifter.

Dispersal

Dispersal in RangeShifter was modelled as three discrete phases of emigration, transfer and settlement. Only post-natal dispersal by juveniles was included, as adults typically show high site fidelity (Yu et al. 2007). Natal dispersal has been considered as a mechanism of prime importance for avoiding inbreeding and competition between relatives in birds (Szulkin and Sheldon 2008). A previous field study found that all the juveniles of the wild crested ibis dispersed from their natal home ranges (Yu et al. 2010). In a preliminary analysis, we found that density-dependent dispersal had little effect on range dynamics, and we therefore assumed density-independent emigration at a fixed emigration probability (Pe) of 0.95, since few cases of philopatric settlement have been observed (Liu 2013).

We modelled the transfer phase assuming individuals disperse stochastically to a distance from their natal site drawn at random from two negative-exponential kernels. The kernels represent common short-distance dispersal and rare long-distance dispersal events, requiring estimates of the mean distance of each kernel (Ds and Dl respectively) and the probability of short-distance dispersal events (P). Ds was fixed at 5.9 km in accordance with field observations (Yu et al. 2010), whereas Dl and P were varied. The suitability of the arrival cell determined whether the dispersal would be successful. If the arrival cell was unsuitable, the individual could move randomly to one of the eight neighbouring cells if any was suitable. If both the arrival cell and all eight neighbouring cells were unsuitable, the individual could wait and disperse again at the next dispersal event in the next year. We assumed no additional dispersal mortality.

Model initialisation, calibration and validation

We used nest site localities in 1994 to initialise the species distribution, and a quasi-equilibrium distribution to initialise the distribution of ages. Parameter estimates were obtained based on literature and expert knowledge, and optimized by fitting the observed and modelled population growth and distribution from 1994 to 2009. We simulated 100 replicates with optimal parameters (see Table 4.1) until 2011 to test model predictions. The modelled population trajectory was visually compared with observed data, and the accuracy of predicted distribution was assessed by the AUC and the TSS. Details about parameterisation, calibration and validation are elaborated in Appendix S1 in Supporting Information.

Table 4.1 The fixed and optimized RangeShifter parameters set for range expansion modelling and their estimated bounds for sensitivity analysis based on the quality of information available (darker grey representing poorer quality of information and consequently greater parameter uncertainty).

Parameter (Unit)	Value	Description	Estimated range
MaxAge	16	Maximum age	–
Φ	2.0	Number of male offspring per male	–
Pe	0.95	Emigration probability of juveniles	–
Ds (km)	5.9	Mean distance of short-distance dispersal	–
P	0.95	Optimal probability of short-distance dispersal events	0.92-0.98
Ss	0.67	Optimal subadult survival probability	0.61-0.71
Sa	0.79	Optimal adult survival probability	0.75-0.84
$1/b$ (ha ⁻¹)	0.055	Optimal strength of density dependence	0.049-0.061
Dl (km)	30	Optimal mean distance of long-distance dispersal	27-33

Future range expansion predictions

We used nest site and population data from 2011 for initialisation, and ran 100 replicates with validated parameters to predict the future breeding-range expansion of crested ibis for 2020, 2030, 2040, 2050 and 2060. We focused on the simulation results dealing with the prediction of species range dynamics, including male population size, total number of occupied cells and range limits (i.e., longitudinal extent and latitudinal extent).

4.2.4 Sensitivity analysis

We evaluated the uncertainty of demographic and dispersal parameters of the individual-based dynamic range model. We assumed no environmental stochasticity, as our focus was to examine the impacts of uncertainty on range expansion simulation results. We focused on five parameters, S_s , S_a , $1/b$, Dl and P , based on a preliminary local sensitivity analysis. The sensitivity analysis was implemented by applying simultaneous parameter perturbations as advocated by Drechsler (1998). The five parameters were varied in a 3^5 factorial design incorporating optimal/validated values and their estimated lower and upper bounds (243 configurations) given the quality of information available (Table 4.1). We performed 100 replicate simulations for each parameter combination. Model configurations that produced the fastest, medium and slowest spatial spread of crested ibis were identified and defined as high, intermediate and low scenarios. We quantified the sensitivity at 2020, 2030, 2040, 2050 and 2060 of three model outputs (male population size, number of occupied cells and species range extent) to the varied parameters. For each model configuration, we obtained the mean value of the three model outputs from the 100 replicates. For each model output, each parameter and each time period, we performed a univariate linear regression of the model output on the parameter. The relative effect of each parameter to variability in predictions was then given by the explained variance of the linear regression models.

4.2.5 Impact of stochastic catastrophes

To investigate the impact of stochastic catastrophes, we included random local extinction probability (the probability that the whole population in a single cell goes extinct in each year) in the model. Given the low population density in a cell, the local extinction probability is a realistic representation of occasional mortality due to illegal persecution, toxic chemical poisoning

and collisions with power lines. We simulated the range dynamics of crested ibis from 2011 to 2060 with the best fitted model in three scenarios of human-induced mortality risk by adding different levels of local extinction probability (i.e., 0.01, 0.03 and 0.05) (see Appendix for an alternative way of incorporating stochastic extinction). We calculated the relative percentage change in population size, number of occupied cells and range extent resulting from a given change in local extinction probability compared with the original model.

4.3 Results

4.3.1 Potential habitat suitability and accuracy assessment

The habitat suitability model produced a mean AUC value of 0.93 ± 0.023 (mean $\pm$ standard deviation, the same hereinafter) and a mean TSS score of 0.83 ± 0.033 , both of which indicate an excellent predictive performance according to the evaluation approach described by Eskildsen et al. (2013). The maximum TSS value was achieved with an optimal threshold of 0.16 for the breeding habitat suitability. Thus, cells with values ≥ 0.16 were considered suitable habitat, and those < 0.16 were deemed unsuitable. Based on the contribution of environmental predictors to increasing the regularized gain in the MaxEnt model, annual maximum NDVI, annual maximum LSWI and minimum temperature of the coldest month were the three most important variables in determining habitat suitability for breeding crested ibis (see Table A4.2 in Appendix). The potential breeding habitat exhibited a patchy distribution, mainly found in the central and southern parts of Shaanxi, north of Henan, Chongqing, and some adjacent areas (Fig. 4.2). The range currently occupied by the breeding crested ibis was somewhat isolated from other potential suitable areas. Scattered habitat fragments extended eastward and westward, and the potential habitats to the north and south were about 70 km and 150 km respectively from the current crested ibis range.

Figure 4.2 Predicted habitat suitability for breeding crested ibis from the MaxEnt model. The area within the rectangle indicates the current range (local range) of breeding crested ibis. Three reintroduction sites are marked with flag symbols.

4.3.2 Range expansion modelling with optimal parameters

The population trajectory predicted using the optimal parameters followed the observed population trend very well (see Fig. A4.1 in Appendix). The simulation of nest site distribution for year 2011 (see Fig. A4.2) produced an AUC score of 0.85 and a TSS score of 0.69, which is considered a good model (Eskildsen et al. 2013). The crested ibis population was predicted to continue to increase in size and expand its range over the next 50 years to around $14,000 \pm 3730$ breeding males and 4370 ± 1060 occupied cells by 2060, increasing by 32 and 50 times, respectively. The breeding range extent

was predicted to increase by 14 times in the coming five decades, and by 2060 the latitudinal and longitudinal extents would have reached 321 ± 54.8 km and 476 ± 50.9 km, respectively. The range was predicted to expand initially westward into the southern adjacent area of Shaanxi and Gansu provinces, and thereafter further to the north and east (Fig. 4.3). Potential habitat to the south appeared unlikely to be reached by natural expansion within the next 50 years. By 2060, the potential breeding range of crested ibis could spread as far as 200-300 km from the current range to the east, west and north. However, high occupancy probabilities were predicted around the current range and much lower probabilities elsewhere. On average, about 54% of the predicted population in 2060 lay within a distance of 50 km of the current local range, and 86% within a distance of 100 km.

Figure 4.3 Predicted range expansion within 300 km of the current local range of breeding crested ibis in years 2020, 2030, 2040, 2050 and 2060. Occupancy probability of a cell was assessed based on 100 replicate simulations. The locations of principal historical records are marked with circled dots.

4.3.3 Impacts of uncertainty in demographic and dispersal parameters

The relative contribution of each parameter to variation in predictions differed between the model outputs and between simulation periods (Table 4.2). The demographic parameters (i.e. S_s , S_a and $1/b$) contributed much more to the variation in population size and number of occupied cells than to the range extent, among which the most influential parameter was either S_a or $1/b$. In general, the impact of uncertainty in demographic parameters on population size and number of occupied cells decreased over simulation time, whereas the impact on range extent increased over time. Variance of population size and number of occupied cells explained by $1/b$ had a greater amplitude compared to the explained variance by survival rates. Unsurprisingly, the dispersal parameters (i.e. DI and P) explained more variance in the range extent. Specifically, P , the probability of short-distance dispersal events, the most influential parameter on range extent, accounted for 58% of variation in predicted range extent in the first decade and 31% in the fifth decade. The effect of P on population size and number of occupied cells increased over simulation time, such that its influence on the number of occupied cells by 2060 matched that of the demographic parameters. Uncertainty in the mean distance of long-distance dispersal had a slightly stronger effect than demographic parameters on range extent and no significant effect on population dynamics. The range expansion process in high, intermediate and low scenarios showed large differences between each other, where the low scenario would trail over 20 years behind the high scenario by 2060 (Fig. 4.4).

4.3.4 Impact of stochastic extinction

There was no significant difference in the model outputs after 50 years between the original simulation and the simulation including low stochastic extinction (i.e., 0.01), no matter by which means it was incorporated in the model. As the local extinction probability increased, it exhibited a significant negative impact on population growth and range expansion of crested ibis (see Figure A4.3 in Appendix). By 2060, mean population size, number of occupied cells and range extent were reduced by 40%, 34% and 16% respectively when local extinction probability was 0.03, and by 58%, 52% and 29% respectively at 0.05 probability (see Table A4.3 for results from the alternative way of including stochastic extinction).

Table 4.2 Sensitivity of key model outputs based on 243 combinations of uncertain parameters, strength of density dependence ($1/b$), mean distance of long-distance dispersal (Dl), probability of short-distance dispersal events (P), subadult survival probability (Ss) and adult survival probability (Sa) (direction of impact shown in parentheses).

Output	Year	Mean	SE	Explained variance by parameter uncertainty (%)				
				$1/b$ (+)	Dl (+)	P (-)	Ss (+)	Sa (+)
Male population size	2020	1250	19.1	38.1	ns*	ns*	26.0	34.4
	2030	3240	61.6	31.2	ns*	ns*	27.6	39.3
	2040	5000	110	28.0	ns*	2.41	25.6	39.8
	2050	8070	252	22.7	1.50	9.11	22.7	33.1
	2060	14740	559	20.9	2.17	13.5	21.9	30.5
No. of occupied cells	2020	492	5.35	40.6	ns*	ns*	26.5	32.5
	2030	993	12.2	32.2	ns*	1.23	27.7	38.1
	2040	1490	24.8	26.0	1.14	7.81	24.6	35.8
	2050	2460	65.6	20.6	2.72	16.5	21.5	29.0
	2060	4300	131	19.7	3.30	20.5	21.2	28.0
Range extent (km ²)	2020	25400	454	9.23	12.7	58.0	5.57	7.14
	2030	53000	1030	8.52	14.2	52.7	7.82	11.0
	2040	79800	1560	9.74	14.1	47.4	8.97	14.5
	2050	110000	2340	10.6	13.2	45.0	9.50	15.9
	2060	146000	3200	10.6	12.2	31.0	10.7	17.1

* ns, no significant contribution of the parameter to variation in predictions

Figure 4.4 Uncertainty in the predicted range expansion within 300 km of the current local range of breeding crested ibis in years 2020, 2030, 2040, 2050 and 2060 due to parameter uncertainty. The selected high, intermediate and low scenarios of model configurations produced the fastest, medium and slowest recolonization by crested ibis, respectively. Occupancy probability of a cell was assessed based on 100 replicate simulations for each scenario.

4.4 Discussion

The crested ibis population has undergone a recent recovery after a period of serious decline. Assuming unchanging environmental conditions, life-history traits and protection status as well as no catastrophic diseases, our study shows that there will be no risk of extinction for the crested ibis in the wild in the next 50 years. It is expected that species increasing in abundance will also increase in range, and this appears to be the overall pattern in recovery for avian species (Deinet et al. 2013). Even though the crested ibis is predicted to expand its geographical range and to recolonize some part of its former range (Fig. 4.3), the majority of the population will still be restricted to a relatively small range. Some potential suitable habitat seems very unlikely to be recolonized naturally by crested ibis, at least in the next few decades. The species might still be at substantial risk from catastrophic changes (e.g., habitat loss, diseases and climate disasters) in Shaanxi.

Understanding the factors that limit species range expansion is crucially important in building effective management and conservation strategies. Adult, and to a lesser extent subadult, survival probability showed a substantial influence on the predicted demographics of crested ibis. Previous studies (G. Bocedi et al. 2014; Heikkinen et al. 2014) have highlighted the important role of carrying capacity in species range dynamics. For a non-equilibrium species, carrying capacity is difficult to estimate; especially as the recovering crested ibis adapts and evolves (Sun et al. 2014). Our study found considerable sensitivity to uncertainty in the strength of density dependence (a principal determinant of carrying capacity in RangeShifter), especially in the first decade when the majority of the crested ibis population would still be restricted to the local range with poor connectivity to potential suitable habitat further away. Therefore, we concur with Heikkinen et al. (2014) that caution must be exercised when setting carrying capacity, especially in a fragmented landscape. On the other hand, researchers have varied carrying capacity as a proxy for assessing the influence of changes in habitat quality and quantity, or both (Naujokaitis-Lewis et al. 2009). A cell with low habitat quality may act as a partial barrier, while many contiguous low-quality cells could act as a full barrier (Marucco and McIntire 2010). As shown for many species, habitat fragmentation and destruction can hamper their dispersal abilities (Collingham and Huntley 2000; Bateman et al. 2013). Likewise, our results also imply that decreasing habitat suitability and availability could have a

negative effect on spatial population dynamics. The isolated and/or small habitat fragments are expected to slow down or even hinder the natural recolonization process of crested ibis, and the consequences can be even worse given that further habitat loss and degradation are inevitable in the face of environmental changes.

Earlier studies have demonstrated that long-distance dispersal may contribute to species persistence in fragmented landscapes (Tittler et al. 2006) and range shifts in response to climate change (Higgins and Richardson 1999). Our results showed that a greater probability of long-distance dispersal events could result in a faster and further range expansion of crested ibis, and indicated that the proportion of long-distance dispersal events could be one of the most influential factors that contribute to the geographical feature of species range dynamics. Ignoring potential long-distance dispersal events in range dynamic modelling may lead to inaccurate predictions, but caution must also be exercised in drawing firm conclusions from a single-sex model in which genetics and inbreeding depression are not represented. Moreover, we also found substantial variation in the strength of effect of this parameter on demographic features between time periods with much weaker effects during the first few decades, which may indicate that long-distance dispersers will not substantially contribute to the establishment of satellite populations beyond the current range when habitat availability is limited and/or fragmented, as shown by Fraser et al. (2015).

By using static spatial predictions from SDMs in spatially explicit simulations of non-equilibrium population dynamics, hybrid modelling substantially improves our ability to predict species range expansion and understand processes affecting the dynamics (Franklin 2010). However, there are some challenges to improve the current modelling framework. The current geographical range reflects only a snapshot of the expected species-environment relationship, and hence it may not allow an estimation of the fundamental niche of species (Guisan and Thuiller 2005). Many threatened species are not in equilibrium with their environment, and therefore their habitat requirements should preferably be based on their distribution in the historical range in order to support viable conservation plans for species recovery. Our prediction of habitat distribution for crested ibis may be underestimated owing to the lack of species data of sufficient precision and of relevant environmental layers prior to the widespread range contraction. The use of historical data may provide us with knowledge of a broader

niche, so that areas with similar ecological characteristics could be occupied again if the species continues to recover and has retained its adaptive ability to this niche and the terroir of the a historical range has not changed. On the other hand, we assumed a constant landscape, species-environment relationship and demographic rates, which may be violated in the case of changes in biotic interactions as well as ecological and behavioural adaptations under changing environmental conditions. Moreover, colonization of the breeding crested ibis can be affected by many other factors, such as food abundance as well as the suitability and proximity of non-breeding habitat. Investigating and taking into account these effects could make range expansion modelling of crested ibis more realistic and precise. In the context of potentially increasing frequency of catastrophic events resulting from extreme weather events under climate change, future work can incorporate the influence of these natural catastrophes on range dynamics modelling of species recovery.

4.4.1 Implications for conservation

Our study demonstrates that a hybrid model for species range expansion, which has been increasingly used in the study of biological invasions (Gallien et al. 2010; Fraser et al. 2015), can assist in conservation management of threatened and endangered, but recovering wildlife populations, as they recolonize their former range. Range expansion modelling provides guidance to allocate conservation resources. Prior to the implementation of recommendations derived from modelling, managers and conservationists must be aware of the uncertainties in model parameterisation that may affect the robustness of predictions. Therefore, long-term monitoring of the key life-history parameters of target species, especially the detection of rare long-distance dispersal events, is necessary for an accurate understanding of spatial population dynamics.

Reintroduction programmes of crested ibis have been carried out for several years (Yamagishi 2009; Yu et al. 2009). The predicted habitat suitability for breeding crested ibis and its potential range expansion pattern provide information on existing reintroduction sites as well as evidence for selection of alternative reintroduction sites. It is worth noting that habitat availability in Ningshan was limited, narrow and fragmented with lower suitability due to the complex topographical conditions, compared to the source population range and the other two reintroduction sites (Fig. 4.2). The reintroduced population in Ningshan has been found to disperse over

longer distances than the original population of crested ibis (Liu 2013), presumably due to larger inter-patch distances. On the other hand, the reintroduction site in Ningshan is within a maximum dispersal distance of the current crested ibis range, as is Tongchuan (Fig. 4.2). It might be argued that it is unnecessary to reintroduce birds to a reachable area, because our results show that even without reintroductions, wild crested ibis will recolonize these areas in time. Nevertheless, from a different perspective, reintroductions to these areas could be considered as an increase to long-distance dispersal events assisted by humans that would have a positive effect on crested ibis range expansion. The reintroduction to Ningshan has been found to stimulate gene exchange with the wild population, and to facilitate the dispersal of the source population to the east (Dong et al. 2010). The reintroduction to Tongchuan is therefore expected to speed up the recolonization to north of the Qinling Mountains and facilitate the establishment of satellite populations. Dispersing crested ibis may face higher human-induced mortality risks in newly colonized areas, where this distinctive bird may be completely unknown to the public. However, being an iconic species, efforts to conserve the crested ibis may be embraced by local communities. Although a low level of human-induced mortality is unlikely to have a significant impact on the recovery and recolonization of crested ibis, the impact of potentially increasing human disturbances should not be neglected.

Appendix

Environmental predictors

Bioclimatic variables

Bioclimatic variables were obtained from the WorldClim database (<http://www.worldclim.org/>), including annual means, seasonality, and extreme or limiting temperature and precipitation data derived from the period between 1950 and 2000. In this study, 19 climatic layers with a spatial resolution of 30 arc-seconds (~1 km) were used (Table A4.1), which are presumed to be biologically meaningful to characterise habitat suitability for crested ibis at a large spatial scale.

Satellite-derived vegetation and water indices

Satellite-derived vegetation and water indices are indicative of favourable habitats and feeding areas for waterbirds and have been used in ecological modelling of their spatial distributions (Cappelle et al. 2010). We obtained 16-composite MODIS 250m Vegetation Indices data (MOD13Q1) over the three year period from 2010 to 2012 from the USGS Global Visualization interface (GloVis, <http://glovis.usgs.gov/>). The time-series Normalized Difference Vegetation Index [NDVI, equal to $(Q_{NIR} - Q_{RED}) / (Q_{NIR} + Q_{RED})$] data were cleaned and smoothed using an adaptive Savitzky-Golay filter (Jönsson and Eklundh 2004) to reduce the potential noise of cloudiness but keep high fidelity of the data. Then, three phenological cycles were reconstructed and one time series of the averaged data were used to calculate several statistical indices, namely annual maximum NDVI, mean NDVI, minimum NDVI, NDVI amplitude (difference between maximum and minimum NDVI) and NDVI standard deviation. We used 8-day composite MODIS 500m Surface Reflectance Product (MOD09A1) from 2010 to 2012 downloaded from GloVis to calculate Land Surface Water Index [LSWI, equal to $(Q_{NIR} - Q_{SWIR}) / (Q_{NIR} + Q_{SWIR})$], using surface reflectance values from the near infrared (NIR, 841-876 nm) and short-wavelength infrared (SWIR, 1628-1652 nm) bands. The same procedure as used for the NDVI was applied to smooth and calculate the annual maximum LSWI, mean LSWI, minimum LSWI, LSWI amplitude (difference between maximum and minimum LSWI) and LSWI standard deviation.

Other environmental variables

We obtained the map of canopy height at 1 km spatial resolution from NASA Jet Propulsion Laboratory (<http://lidarradar.jpl.nasa.gov/>). It is a global product derived from the Geoscience Laser Altimeter System (GLAS) lidar data (Simard et al. 2011), and presumed to be associated with species habitat selection in terms of vertical structure. Elevation data, which illustrate topographic features of the habitat, were obtained from the global 30 arc-second (~1 km) digital elevation model (GTOPO30) via USGS EarthExplorer (<http://earthexplorer.usgs.gov/>). Gridded human population density data, as a proxy of human disturbance, at a resolution of 30 arc-seconds (~1 km) were obtained from NASA Socioeconomic Data and Applications Center (<http://sedac.ciesin.columbia.edu/data/collection/grump-v1>).

All these variables used in the habitat suitability modelling are shown in Table A4.1. All spatial data were projected using the Lambert azimuthal equal-area projection, resampled to 1 km resolution.

Evaluation of the performance of MaxEnt

The accuracy of the model prediction of habitat suitability was evaluated by the area under the receiver operating characteristic curve (AUC) and the true skill statistic (TSS). As a threshold-independent method, AUC ranges from 0 to 1, where 1 indicates perfect discrimination between occupied and unoccupied sites, and 0.5 or less indicates discrimination no better than random. The TSS, a threshold-dependent method, takes into account sensitivity and specificity, whilst not being sensitive to prevalence (Allouche et al. 2006). The TSS ranges from -1 to 1, where 1 indicates perfect discrimination and 0 or less indicates discrimination no better than random.

Processes for habitat suitability map used in range expansion modelling

The model landscape was modified to make the availability of suitable breeding habitat more realistic. Cells below the suitability threshold of 0.16 (which resulted in the maximum sum of sensitivity and specificity) were deemed unsuitable and assigned value of zero (as required by RangeShifter when using a habitat quality index landscape). This was to prevent dispersing birds from settling in very low quality areas where they are unlikely to reproduce. Instead, if dispersing individuals land in unsuitable

habitat, they will move to a randomly selected neighbouring cell of suitable habitat if available, otherwise they could wait for the next dispersal event in the next year. The habitat suitability was then rescaled ranging from 0.0 to 100.0 as an input requirement of Rangeshifter.

Parameterisation, calibration and validation for the range expansion model

We used nest site localities in 1994 to initialise the species distribution, and estimated the number of individuals per cell and the proportion of subadults and adults from the population monitoring data. We used a quasi-equilibrium distribution to initialise the distribution of ages, which are set approximately in accordance with the number of years taken to pass through the stage and the survival rate of the stage.

For demographic and dispersal parameters, we first estimated their plausible ranges based on literature and expert knowledge. For a non-equilibrium species, carrying capacity is difficult to estimate; especially as the recovering crested ibis is adapting and evolving. Crested ibis breeding territories used to occupy a whole valley when the species was restricted to suboptimal habitat (Ding 2004). As the population has increased and expanded into areas having more resources, territory size has reduced, and it has been observed that several nests were located close to each other in a same tree (Shaanxi Hanzhong Crested Ibis National Nature Reserve et al. 2010). Previous population viability analysis of the wild crested ibis (Li 2013) estimated the population size at equilibrium in the local range (Yang County) to be 2108 ± 500 . We tested the range of values for the parameter $1/b$ (which controls the level of density dependence in fecundity, and hence carrying capacity) from 0.045 to 0.065 ha^{-1} . We estimated plausible ranges for survival rates based on empirically observed data on age-specific mortality in the wild population (Wang, Wang, et al. 2000). Subadult survival probabilities from 0.61 to 0.71 and adult survival probabilities from 0.75 to 0.84 were tested. We estimated the mean dispersal distance and proportion of long-distance dispersal events from nest site data, of which some were identified to be rare long-distance dispersal events based on expert knowledge. We used values of 25 km, 30 km, 35 km and 40 km for the mean distance of long-distance dispersal and values of 0.92 to 0.98 for the probability of short-distance dispersal events. The mean distance of short-distance dispersal was fixed at 5.9 km based on empirical results from Yu et al. (2010).

We then improved demographic parameter estimates by fitting the model to the observed early population growth during the first 15 years of range expansion from 1994 to 2009. We ran 100 replicates for each scenario of dispersal parameter combinations, and the probability that a cell was occupied after 15 years was calculated across replicates. We compared the observed distribution of nest sites with the predicted occupancy probability for each dispersal scenario and identified the scenario having the best match determined by the highest TSS. As a result, the optimal parameters for subadult survival probability and adult survival probability were 0.67 and 0.79, respectively. The strength of density dependence was 0.055 ha^{-1} when the model achieved the best fit (TSS=0.73). The mean distance of long-distance dispersal was optimized at 30 km, and the probability of short-distance dispersal events at 0.95.

We simulated 100 replicates with optimal parameters (see Table 4.1) until 2011, two years past our calibration phase, to test our model predictions. We calculated means and standard deviations of male population size over all replicated runs for each year and visually compared modelled and observed data. We identified those cells which had at least one adult male present, and assumed that they defined the presence of nest sites (i.e. breeding range). The predicted probability map of nest site distribution in 2011 was then obtained by averaging all replicate raster maps of adult male presence. The accuracy of predicted nest site distribution was evaluated using both the AUC and the TSS. Nest site localities in 2011 were used as presence points, and the same number of pseudo-absence points were randomly generated within the suitable habitat in the local range.

Alternative way of incorporating stochastic extinction

In addition to adding different levels of local extinction probability (i.e., 0.01, 0.03 and 0.05) to the model, we increased adult survival probability to the same degree as local extinction probability to allow for the modelling of catastrophic mortality separately, as it could be argued that the observed survival rate already allows for such mortality risks. The model outputs generated by three scenarios of local extinction and two ways of incorporating stochastic extinction as well as the original simulation were compared using pairwise Mann-Whitney U tests.

Table A4.1 Environmental variables used for modelling the habitat suitability for breeding crested ibis.

Category (Data source)	Variable	Unit
Bioclimate (WorldClim)	Annual mean temperature	°C
	Mean diurnal range	°C
	Isothermality	Dimensionless
	Temperature seasonality	°C
	Max temperature of warmest month	°C
	Min temperature of coldest month	°C
	Temperature annual range	°C
	Mean temperature of wettest quarter	°C
	Mean temperature of driest quarter	°C
	Mean temperature of warmest quarter	°C
	Mean temperature of coldest quarter	°C
	Annual precipitation	mm
	Precipitation of wettest month	mm
	Precipitation of driest month	mm
	Precipitation seasonality	Dimensionless
	Precipitation of wettest quarter	mm
	Precipitation of driest quarter	mm
	Precipitation of warmest quarter	mm
	Precipitation of coldest quarter	mm
Vegetation (MODIS)	Annual minimum NDVI	Dimensionless
	Annual mean NDVI	Dimensionless
	Annual maximum NDVI	Dimensionless
	NDVI Amplitude	Dimensionless
	NDVI Standard deviation	Dimensionless
Water (MODIS)	Annual minimum LSWI	Dimensionless
	Annual mean LSWI	Dimensionless

Table A4.1 (Continued).

Category (Data source)	Variable	Unit
(MODIS)	LSWI Amplitude	Dimensionless
	LSWI Standard deviation	Dimensionless
Vegetation (GLAS)	Canopy height	m
Topography (GTOPO30)	Elevation	m
Population (GRUMP)	Human population density	km ⁻²

Table A4.2 Percentage contribution of predictors to MaxEnt model gain for habitat suitability for breeding crested ibis. Model gain is the average log probability of the presence samples minus a constant. Only the variables with over one per cent contribution are reported here.

Variable	Percentage contribution
Annual maximum NDVI	25.5
Annual maximum LSWI	13
Min temperature of coldest month	10
LSWI Amplitude	7.2
Mean diurnal range	6.1
Canopy height	5.2
Precipitation of wettest month	4.6
Precipitation of warmest quarter	4.4
Human population density	4.2
NDVI Standard deviation	3.9
Isothermality (BIO2/BIO7)	2.9
Annual precipitation	2.4
Annual mean NDVI	2.3
Annual minimum LSWI	1.9
Annual minimum NDVI	1.6
Mean temperature of coldest quarter	1.5

Table A4.3 Outputs of models for 2060 including stochastic extinction and the relative change compared with the original model

Model	Male population size		No. of occupied cell		Range extent	
	Mean	Relative change	Mean	Relative change	Mean	Relative change
Original	13967	-□	4366	-□	152796	-□
LEP1-0.01	13151	-5.8%	4169	-4.5%	149621	-2.1%
LEP1-0.03	8381	-40.0%	2867	-34.3%	128986	-15.6%
LEP1-0.05	5860	-58.0%	2101	-51.9%	108356	-29.1%
LEP2-0.01	13551	-3.0%	4240	-2.9%	153584	0.5%
LEP2-0.03	11322	-18.9%	3634	-16.8%	142512	-6.7%
LEP2-0.05	9028	-35.4%	2987	-31.6%	133383	-12.7%

LEP1, adding a local extinction probability (0.01, 0.03, 0.05) to the original model

LEP2, increasing adult survival rate by the same amount of local extinction probability

Figure A4.1 Trajectories for observed (closed squares) and predicted (open circles) male population size. Error bars represent the standard deviation calculated across 100 replicates.

Figure A4.2 Predicted nest site distribution of the crested ibis for year 2011. Occupancy probability of a cell was assessed based on 100 replicate simulations. The locations of nest sites in 2011 are marked with black dots.

Figure A4.3 Boxplots showing differences in three key modelling outputs between the original model and models with an extra local extinction probability (LEP1) and models with increased adult survival rate by the same amount of local extinction probability (LEP2). The pairs with no significant difference are annotated based on pairwise Mann-Whitney U tests ($p > 0.05$).

Chapter 5

Predicting Crested Ibis Distribution under Climate and Land-Use Change

This chapter is based on: Sun, Y., T. Wang, A.K. Skidmore, C. Ding, and X. Ye. 2016. Predicting crested ibis distribution under climate and land-use change. *Scientific Reports* (resubmitted after revision).

5 Predicting crested ibis distribution under climate and land-use change

Abstract

The crested ibis (*Nipponia nippon*) has experienced a dramatic population decline due to historical anthropogenic factors, and currently persists in a small fragment of its former range. Adequate conservation requires knowledge of the natural history and biology of the species as well as information on habitat availability. However, such background knowledge and information are simply lacking for the crested ibis, which prevented us from developing a long-term and realistic conservation plan. We used species distribution models within an ensemble forecasting framework to establish the historical baseline range of the crested ibis and to project its future potential distribution under climate and land-use change. We quantified the niche similarity between seasons to investigate the migratory behaviour of the crested ibis and examined the niche stability over time. Our results provided a more precise depiction of historical crested ibis distributions in breeding and wintering seasons, and the pattern was generally consistent with the literature. The crested ibis was partially migratory in the past and seemed to track similar niches while seasonally migrating. Similar but non-equivalent niches as well as different impacts of environmental variables indicated a change in the realized niches of crested ibis through time. Based on the niches observed in both the past and present, the potential suitable areas for crested ibis were expected to encounter a northward shift under future environmental change, with a contraction in both breeding and wintering ranges compared to historical baselines. The use of historical information provided a more robust assessment of species distributions in geographical and ecological space, and obtained more reliable information than the speculative conclusions derived from limited field data, which can be used to guide the conservation of endangered species such as the crested ibis.

5.1 Introduction

Many species have experienced dramatic population decline and range contraction (Kuemmerle et al. 2012; Deinet et al. 2013). Some have become extirpated regionally, and persist in small fragments of their original distribution ranges as a result of human-induced habitat destruction and overhunting (Deinet et al. 2013). The current geographical ranges of these species only reflect a snapshot view of the expected species-environment relationship, hence does not allow an estimation of the fundamental environmental requirement. Furthermore, these areas do not necessarily represent the species' optimal environmental conditions (Caughley 1994). Efficient conservation not only requires detailed knowledge of the natural history and biology of the species, but also information on range-wide habitat availability and suitability. In such cases, establishing a historical baseline range prior to the range contraction caused by widespread human disturbance may result in a more robust assessment of species distribution (Nogués-Bravo 2009). A better understanding of species distribution and its environmental requirements in the past is essential to inform us about the current state of the species and its potential response to future environmental change.

Occurrence data for the vast majority of species are scarce, and knowledge of species' historical distributions may be as superficial as a few names of locations or oversimplified range maps outlined based on written records. These data present a far-from-complete picture of species distribution, thus is inadequate for proper scientific analyses and conservation planning. Species distribution models (SDMs) offer a means to extrapolate limited information for an estimation of the distribution over large areas. Some applied ecological studies have made use of museum data and historical literature to investigate the past distribution of species, and incorporated it in large-scale conservation strategies (e.g., Kuemmerle et al. 2012; Clavero and Hermoso 2015).

Climatic and land-use changes have been shown to alter species' geographical distributions (e.g., Ficetola et al. 2010; Auer and King 2014; Gillings et al. 2015), and have become important factors to consider in conservation plans. When projecting SDMs under different scenarios of future climatic or/and land-use change, the assumption of niche stability has been taken for granted in many studies without critical considerations (but see Maiorano et al. 2013). Niche stability assumes non-significant

evolutionary or/and ecological changes in a species niche as a response to changing environmental conditions through time. However, evidence suggests that niche shifts may have occurred in some species as a result of genetic variation in traits related to environment or competition with different species at different time (Broennimann et al. 2007; Nogués-Bravo 2009). The deviation from the niche stability assumption may limit the model predictive performance and model transferability in time, resulting in improper or inadequate conservation assessments and plans for species. Among different approaches that have been suggested to overcome the problem, ecological niche obtained through multi-temporal calibration not only allows quantitative assessment of niche stability, but also provides a better approximation of the fundamental niche or at least a more complete realized niche than observed at a single time frame (Maiorano et al. 2013).

The crested ibis (*Nipponia nippon*) was originally widespread in East Asia, but the population declined severely in the mid-twentieth century, leading to extirpations throughout almost all of its former range (BirdLife International 2012). The relict population has been restricted in the Qinling Mountain region of China. Considerable efforts have been made to protect this endangered species and its habitat, and reintroductions have been carried out in few sites in China and Japan (Yu et al. 2009; Mochizuki et al. 2015). Although knowledge about this species is much improved based on the relict population, the historical distribution has been under debate due to the lack of observation records, and we know little about relationships between crested ibis distribution and environmental changes. Moreover, the relict population is sedentary with local-scale seasonal movement (Ding 2010), but it is presumed that the birds from Russia and Northeast China migrated to the Korean Peninsula over winter in history (BirdLife International 2001). To cope with seasonal changes in environment conditions, species may chase a consistent climatic regime via seasonal movements (niche tracking) (Nakazawa et al. 2004; Marini et al. 2010), or exhibit seasonal variation in its ecological niche (niche switching) (e.g., Marini et al. 2013; Laube et al. 2015; Lunghi et al. 2015). Unfortunately, neither the seasonal distributions nor the migratory behaviour of the crested ibis has been understood.

The overall objective of this study was to understand the historical crested ibis geographical distribution and niche characteristics at a broad scale, and to predict the potential distribution under future environmental change. Specifically, we used SDMs within an ensemble forecasting framework to

reconstruct the historical baseline range of the crested ibis. We investigated the migratory tendency and the niche similarity between seasons for crested ibis. We examined the niche stability from the past to present, and predicted the future potential distribution under climate and land-use change based on the niches observed historically and at present.

5.2 Methods

5.2.1 Study area and species data

The study area includes the entire historical distribution of crested ibis i.e., the Russian Far East, China, Japan and the Korean Peninsula, located between 17°N to 57°N and 95°E to 150°E (Fig. 5.1). According the historical records, the crested ibis used to nest in the Russian Far East, Japan and China, and was a non-breeding visitor to North Korea, South Korea and Taiwan (China) (BirdLife International 2001). It breeds during February to June (Ding 2010), nesting in tall trees near to wetlands or agricultural land for feeding (Sun et al. 2014). In winter (November to January), the main habitats include rice fields, river banks or reservoirs near human settlements (Ding 2010).

Occurrence data of the crested ibis were obtained from (1) field observations with high precision from a long-term monitoring programme conducted by Shaanxi Crested Ibis Nature Reserve since 1981, and (2) published maps and written records (BirdLife International 2001; Shi and Cao 2001; Mochizuki et al. 2015). The occurrence points from published documents were digitized and geographically referenced based on the description of a given locality, high-resolution satellite images from Google Earth and expert knowledge. The occurrences were georeferenced in the WGS 1984 coordinate system. Localities lacking sufficient information for georeferencing (n=8) were discarded. Overall, we obtained 178 records, and we divided them into breeding (n=74) and wintering (n=104) records and into the historical (pre-1950, most of the records were collected after 1900) (n=124) and modern (post-1950) (n=54) periods (Fig. 5.1). Species data in each season of a certain period were plotted in 0.5-degree (~55 × 55 km²) grid cells, removing duplicate presence records within a cell.

Figure 5.1 Locations of the study area and occurrences of the crested ibis during breeding (February-June) and wintering (November-January) seasons in historical (pre-1950) and modern (post-1950) periods.

5.2.2 Environmental variables

Temperature and precipitation data from 1901 to 2014 covering global land surface at a 0.5-degree spatial resolution were obtained from the CRU TS v. 3.23 dataset, available from the Climate Research Unit (<http://www.cru.uea.ac.uk/>, Harris et al. 2014). We calculated the following eight climatic variables: (1) mean temperature, (2) minimum temperature of the coldest month, (3) maximum temperature of the hottest month, (4) temperature seasonality, (5) mean precipitation, (6) precipitation of the wettest month, (7) precipitation of the driest month, and (8) precipitation seasonality. The seasonality is the coefficient of variation of the monthly means. We used the mean values of these variables calculated for the three peak breeding (March-May) and wintering (November-January) months, as well as variables calculated for an annual cycle, over the historical (1901-1950) and modern (1951-2000) periods.

Future climate predictions at a 10-min resolution were obtained from the CCAFS-GCM Downscaled Data Portal (<http://ccafs-climate.org/>). Given the uncertainty in the projection of future climate, we calculated abovementioned climatic variables for 2080s (2071-2100) for three general circulation models (GCMs; BCC-CSM1.1, CanESM2 and CSIRO-Mk3.6.0). For each GCM, we considered three Representative Concentration Pathways (RCP) scenarios (RCP 2.6, RCP 4.5 and RCP 8.5). The RCPs, adopted by the Intergovernmental Panel on Climate Change (IPCC) for its fifth Assessment Report in 2014, have been considered the most advanced simulations available of global climate system response to changes in radiative forcings as well as different combinations of economic, technological, demographic, policy, and institutional futures (Moss et al. 2010). All climatic layers were resampled to the 0.5-degree resolution using a bilinear interpolation.

Harmonized global land-use data represent fractional land-use patterns and underlying land-use transitions annually for the years 1500-2100 at a 0.5-degree spatial resolution (Available at https://daac.ornl.gov/VEGETATION/guides/Land_Use_Harmonization_V1.html). Historical land uses (1500-2005) were reconstructed based on HYDE data (Klein Goldewijk et al. 2011), and future scenarios (2006-2100) were projected based on the Integrated Assessment Model (IAM) implementations of the RCPs. We only used the variables of fractional land-use patterns (i.e., primary land, secondary land, cropland, pasture and urban) in this study, based on a preliminary analysis of the contribution of the total 32 variables for crested ibis distribution modelling. We used the mean values of these variables for the historical (1901-1950) and modern (1951-2000) periods. For future scenarios, land-use variables based on scenarios of RCP2.6, RCP4.5 and RCP 8.5 were derived from the IMAGE model, GCAM model and MESSAGE model, respectively. The mean values of the five land-use variables were calculated over the period of 2071-2100.

5.2.3 Species distribution modelling

To account for methodological uncertainties in SDMs, we used an ensemble forecasting approach implemented in BIOMOD2 package (Thuiller et al. 2009) in R (R Core Team 2014). We used nine modelling techniques provided by BIOMOD2, including artificial neural networks (ANN), classification tree analysis (CTA), flexible discriminant analysis (FDA), generalized additive models (GAM), generalized boosting models (GBM,

also known as boosted regression trees), generalized linear models (GLM), multivariate adaptive regression splines (MARS), maximum entropy (MaxEnt) and random forests (RF). In addition to several widely used regression techniques (e.g., GLM, GAM, and MARS), a number of more modern machine learning algorithms (e.g., RF, BRT, and MaxEnt) were implemented, which may offer better predictive performance for non-linear relationships compared to traditional algorithms (Elith and Leathwick 2009). Both presence and absence data were needed for these SDMs except MaxEnt. As an alternative for lack of true absence data, we randomly generated 1000 pseudo-absences located at least two degrees away from any presence point. This method of pseudo-absence selection for SDMs has been shown to yield better results when few presences are available from the actual distribution (Barbet-Massin, Jiguet, et al. 2012).

We calibrated models with a random sample of 70% of the original data, and assessed model performance with the remaining 30% of the data by measuring the area under the receiver operating characteristic curve (AUC) (Swets 1988). Model performance was considered excellent for AUC values between 0.9-1, good between 0.8-0.9, fair between 0.7-0.8, poor between 0.6-0.7 and failed between 0.5-0.6 (Swets 1988). The entire procedure was repeated 10 times allowing for the calculation of an average AUC value for each model and for both breeding and wintering seasons during different time frames. The final calibration of each model (one for each modelling technique considered) used 100% of the data available. For each season and each period considered, we obtained a final consensus forecast of species distribution calculated as the unweighted average of the three best models. We transformed the continuous consensus forecasts into binary predictions using a threshold that maximized the sum of sensitivity and specificity (Liu et al. 2005). Cells with values greater than or equal to the threshold were considered to be suitable habitat, and those below the threshold were deemed unsuitable habitat. We kept the probabilities for suitable areas, and fixed the probabilities to zero for unsuitable areas.

For the future projection, we calibrated the SDM coupling all occurrences in the historical and modern periods with the environmental responses of the corresponding time frame. The best three models were projected on to the future climate and land-use data for both seasons. For each season, we have 27 estimations ($3 \text{ models} \times 3 \text{ GCMs} \times 3 \text{ RCPs}$) of the future distribution for 2071-2100. In order to obtain the central tendency of these distributions, accounting for variations among climate models and scenarios, we also

used an ensemble forecasting approach to obtain one final future consensus from the unweighted average of 27 modelled distributions. We characterized the potential distributions at different time frames by their ranges and positions (latitude and longitude of the predicted range centroid). We estimated change in the coverage of potential suitable areas over time, and the distance and direction between the range centroids of different time frames.

5.2.4 Niche overlap, equivalency and similarity

To assess the similarity of climatic niches between seasons as well as between the past and present, we considered the framework using an ordination technique for quantifying niche overlap as demonstrated by Broennimann et al. (2012). This framework extends the methods based on SDMs in Warren et al. (2008), allowing hypothesis tests that correct for the spatial autocorrelation in the environment (Warren et al. 2008). For each period, we conducted a principal component analysis (PCA) of the climatic variables described above for both breeding and wintering seasons. The total environmental space was represented by the first two axes of the PCA, and divided into a grid of 100×100 cells. Each cell corresponds to a unique vector of environmental conditions present at one or more sites in geographical space. A kernel density function was applied for the smoothed density of available environments and species occurrences in each cell in the environmental space for each dataset (See Fig. 5.2 as an example). Based on species occupancy of the environment derived from niche and occurrence density, we calculated the Schoener's D statistic (Schoener 1970; Warren et al. 2008; Broennimann et al. 2012) to quantify niche overlap between seasonal ranges or between time frames. The value of D ranges from 0 (no overlap in the environmental space) to 1 (same environmental space).

The niche equivalency test was used to test whether year-round climatic niches between breeding range and wintering range were interchangeable, which can be used to infer the migratory tendency of the species (Marini et al. 2013). The niche overlap statistic D was compared to a null distribution of 100 simulated values of D by randomly reallocating the occurrences among the two ranges. We determined non-equivalence of niches if the observed value of D fell below 95% of the null distribution. The niche equivalency test was also used to compare the seasonal niches occupied by crested ibis between breeding and wintering ranges. As the equivalency test is conservative, we then performed a niche similarity test to examine

whether the seasonal niches were more similar than expected by chance. The similarity test was also based on 100 repetitions. If the observed overlap was greater than 95% of the simulated values, the crested ibis occupied environments in two seasonal ranges that were more similar to each other than expected by chance.

We separated the occurrence records of the crested ibis in the Russian Far East, Northeast China and the Korean Peninsula from the rest (only for the historical period due to the limited occurrence in this area in the modern period), as the historical seasonal distributions were spatially isolated in this area (see Results) and the population was hypothesized to be historically migratory. The equivalency and similarity tests were repeated for the two subsets of the occurrences. To determine whether the difference in climatic niche of the migrant crested ibis between breeding and wintering seasons was reduced as a result of migration, we compared the observed niche overlap (analogous to the intersection of Figs. 5.2a and 5.2d) to the one resulted from alternative hypothetical resident strategies [i.e., assuming crested ibis was resident in the breeding range (analogous to the intersection of Figs. 5.2a and 5.2b) or wintering range (analogous to the intersection of Figs. 5.2c and 5.2d)].

As for niche stability from the past to present, the niche equivalency and similarity tests were performed to assess the degree of shared niches between historical and modern periods for both breeding and wintering seasons. All analyses of niche characteristics were also performed in R platform.

Figure 5.2 Visualization example of occupied and available niche of the presumed migratory subpopulation of crested ibis in environmental space, based on the principal component analysis quantifying the variation in climate during breeding (March-May) and wintering (November-January) seasons. Grey shading shows the grid cell density of species occurrences. Solid and dashed contour lines represent 100% and 50% of the available environment, respectively. Panels **a-d** represent occupied niche space during breeding season (**a**), niche availability in breeding range during wintering season (**b**), niche availability in wintering range during breeding season (**c**), and occupied niche space during wintering season (**d**).

5.3 Results

5.3.1 Historical and modern distributions

Table 5.1 Model performance evaluated by the area under the receiver operating characteristic curve (AUC) of the best three models, the most relevant environmental variables and the threshold maximizing the sum of sensitivity and specificity.

Period	Season	AUC (Mean $\pm$ SD)	Most relevant variables*	Threshold
Historical	Breeding	0.95 $\pm$ 0.02	prec_max, tmp_mean, cropland	0.30
	Wintering	0.94 $\pm$ 0.01	tmp_mean, cropland, primary land	0.24
Modern	Breeding	0.94 $\pm$ 0.00	tmp_min, prec_cv, primary land	0.31
	Wintering	0.97 $\pm$ 0.01	tmp_mean, cropland, secondary land	0.32

*The three variables with the highest contributions are presented, and tmp_mean, tmp_min, prec_max and prec_cv represent mean temperature, minimum temperature of the coldest month, precipitation of the wettest month and precipitation seasonality, respectively.

The three best models selected to estimate the consensus prediction for each season and period had an average AUC value higher than 0.94 (Table 5.1, see Table A5.1 in Appendix for accuracy of all models), indicating that all selected models had an excellent performance. The potential suitable areas for different seasons and periods all exhibited patchy distributions (Fig. 5.3). In the historical period, the predicted suitable areas for breeding were mainly distributed in the Northeast, East and Central China, Japan and the border region of Northeast China and the Russian Far East. Most parts of Japan were suitable for crested ibis to overwinter except for the Hokkaido region. Wintering habitat in East and Central China had a similar distribution range to the breeding habitat, with a southward expansion to the coast and Taiwan. Northeast China and the Russian Far East were not suitable for crested ibis in winter, but a large area of the Korean Peninsula provided highly suitable habitat for overwintering. In the modern period, the potential breeding habitat increased in Central China, but reduced sharply in Northeast China, the Russian Far East and Japan. For the wintering habitat, most of the suitable areas in Japan, South Korea and East

China had disappeared in the modern period, but the highly suitable habitat in Central China remained.

Figure 5.3 Predicted suitable areas for the crested ibis during breeding (a, c, e) and wintering (b, d, f) seasons in historical (a, b), modern (c, d) and future (e, f) periods. The colour chart represents the probabilistic niche suitability in a grid cell above the threshold maximizing the sum of sensitivity and specificity, from low (light yellow) to high (dark brown).

Both climate and land-use patterns contributed in determining the niche suitability for crested ibis, but the most important variables varied between seasons and over time (Table 5.1). In general, mean temperature and the composition of cropland made a considerable contribution to the niche modelling of crested ibis for both seasons and both periods. The responses of crested ibis to the composition of cropland were similar between seasons; however, they showed quite different patterns in different periods (Fig. 5.4). Specifically, the crested ibis preferred a larger area of cropland in the historical period. Both temperature and precipitation were important for the niche suitability for the breeding season in the modern period, but different characteristics of the climate, in terms of trends, seasonality and extreme factors, dominated the distribution pattern in different periods. On the other hand, precipitation was not that important for crested ibis in winter.

Figure 5.4 The response curves of (a) breeding and (b) wintering crested ibis plotted for cropland in historical and modern periods based on the SDMs with best performance. The x-axis represents the range of cropland fraction of each grid cell, and the y-axis represents the predicted suitability when the remaining variables are set to the mean.

5.3.2 Migratory tendency and niche similarity between seasons

The similarity measures for the year-round climatic niches between breeding range and wintering range in the historical and modern periods were $D_{\text{historical}}=0.81$ and $D_{\text{modern}}=0.64$, respectively. For both periods, the year-round climatic niches between seasonal ranges were considered to be identical as we could not reject the null hypothesis ($p_{\text{historical}}=0.89$ and $p_{\text{modern}}=0.44$), indicating the crested ibis was resident or at the most partially migratory as a whole. The seasonal niches exhibited 48% of overlap in historical period and 36% of overlap in modern period. Although not identical, the similarities between seasonal niches were significantly higher than expected by chance (Table 5.2).

Table 5.2 The overlap, similarity and equivalency of climatic niches occupied by the whole population of crested ibis between seasons and over time.

Period /Season	Niche for comparison		Niche overlap (<i>D</i>)	Niche similarity		Niche equivalency
	a	b		a→b	b→a	
Historical	Breeding	Wintering	0.48	ns	similar*	different*
Modern	Breeding	Wintering	0.36	similar*	similar*	different*
Breeding	Historical	Modern	0.49	similar*	ns	different*
Wintering	Historical	Modern	0.52	similar*	similar*	different*

*statistically significant ($p < 0.05$)

ns, not significantly different

The year-round climatic niches between seasonal ranges for the population in the Russian Far East, Northeast China and the Korean Peninsula were not equivalent ($D=0.32$, $p=0.019$), suggesting the birds were migratory in these areas. For the remnant population, the similarity measures for year-round climatic niches between seasonal ranges were much higher ($D=0.82$). Given the null distribution, we could not reject the hypothesis that they were significantly different ($p=0.515$). Similar to the results obtained for the whole population, the seasonal niches occupied by the remnant population were not identical but more similar than expected by chance ($D=0.44$). For the migratory subpopulation, the seasonal niches exhibited 52% overlap, and the null hypothesis of the niche equivalency test could not be rejected ($p=0.059$). Moreover, the climatic niche overlap between breeding and

wintering ranges for the migratory subpopulation ($D=0.51$) was higher than if the birds remained year-round either in the breeding range ($D=0.29$) or in the wintering range ($D=0.17$).

5.3.3 Niche stability from the past to present

As for niche stability over time, the null hypothesis of niche equivalency test was rejected for both seasons, but the null hypothesis of niche similarity test held (Table 5.2). The results suggested that the climatic niches of the crested ibis occupied in the historical and modern periods were more similar than expected by chance, but still not equivalent.

5.3.4 Future distribution under environmental change

The potential breeding habitat was projected to remain with a similar size during the modern period, but it reduced by 30% compared to the historical range. The suitable areas for wintering in the 2080s were predicted to shrink by 18% compared to the historical range. In addition to the change in suitable area, habitat in Central China for both seasons would become less suitable than before (Fig. 5.3). A general northward shift was predicted. Some areas in the Northwest China would become suitable for breeding and the Hokkaido region in Japan would become suitable for wintering, whereas habitats in South China would become unsuitable in the future. Compared with the present range, the potential breeding distribution was projected to shift 570 km northward, and the potential wintering distribution shift 939 km to the northeast.

5.4 Discussion

5.4.1 Predictions using the historical baseline

Extinct population records were used to predict the original geographical distribution of the crested ibis. In general, the predictions are consistent with the historical range described in the literature (BirdLife International 2001; Shi and Cao 2001), specifically that the crested ibis bred in the Russian Far East, Japan and mainland China, and visited the Korean Peninsula and Taiwan in winter. A few scholars inferred that crested ibis might breed in the Korean Peninsula and Taiwan in spite of lack of substantiated records (reviewed by Shi and Cao 2001). Our results may help

to reassure scholars that it was hardly possible for crested ibis to breed in these areas without any suitable habitat. Moreover, the reported occurrence in Hainan Island deemed as the southernmost record of crested ibis (reviewed by BirdLife International 2001) was likely to be incorrect.

Species survival is affected by threats occurring in both breeding and wintering areas (Walther et al. 2007; Newton 2008). Decreases of breeding populations of many species could be been linked to poor environmental conditions in the wintering areas (Newton 2008; Zwarts et al. 2009). It was reported that the habitat for winter feeding in the range of the relict population of crested ibis in Central China had reduced by almost 90% between the 1950s and 1980s (Dong et al. 1992; Sun et al. 2015). Apart from human persecution and hunting, the decrease in the suitable areas due to global warming and land-use change could exacerbate the decline of the crested ibis population (Ding 2004; Li et al. 2009).

Climatic variables have been considered the main drivers of broad-scale diversity patterns (Hawkins et al. 2003). Our study showed that land-use pattern also played an important role in determining the distribution of crested ibis at a broad scale. It is not surprising that the crested ibis was associated with cropland. As a typical feature in East Asia, paddy fields for growing rice and other semiaquatic crops have served as essential anthropogenic habitats for wading birds, similar to those of natural wetlands in both breeding and wintering seasons (Elphick 2000). The traditional Asian rice cultivation system involves a single crop per year and fallow flooding over a long period, which provides ideal food resources for crested ibis. However, agricultural practices have been greatly intensified in East Asia since World War II (Tyson et al. 2002; Wood et al. 2010; Katayama et al. 2015). The decrease in the suitability of areas with more cropland for crested ibis is probably related to modifications in agricultural practices in the modern period. Agricultural intensification through expanding cropland and clearing natural vegetation may decrease the landscape heterogeneity, which is considered a major driver of the loss of biodiversity and associated ecosystem services (Tilman et al. 2001). Moreover, modernization and intensification of farming practices through increased agrochemical usage and improved farming conditions have a stronger negative impact on the crested ibis population (Wood et al. 2010; Katayama et al. 2015). The impact of pesticides was greatest in the 1950s–1970s until the highly persistent and toxic chemicals were prohibited successively in

most of the Asian countries (Wood et al. 2010; Katayama et al. 2015). Agricultural machinery and efficient irrigation/drainage systems have facilitated multiple cropping and shortened fallow period in enlarged and more regularly spaced fields (Katayama et al. 2015). These have resulted in decreased feeding and breeding opportunities as well as higher risks of mortality. The preference for primary land (i.e., land with natural vegetation that has not been subject to human activity) by crested ibis during the breeding season in the modern period may also indicate a decrease in the suitability of cropland and an increase in human disturbance compared to the historical period. The traditional agricultural systems of smallholder farmers in more marginal and fragile areas such as mountains or hills (Wood et al. 2010; Sun et al. 2015) probably provides a last refuge for the relict crested ibis population.

Although broad-scale biogeographical data used in SDMs can provide valuable insights into species responses to the environment, only certain broad-scale aspects of a species' niche are captured. Habitat is defined at finer scales, and such habitat information is usually not available for the entire range at larger scales, such as the distribution of winter-flooded rice fields. Our models and analyses were also limited by the unavailability of other factors affecting the habitat suitability for crested ibis, such as the presence of tall trees, human disturbance and environmental pollution. Additionally, the potential distribution could be further influenced by species interactions and dispersal ability.

5.4.2 Seasonal niches and migratory behaviour

For species with a broad distribution, populations can experience different environments that lead to variations in life-history strategies (Hansson and Akesson 2014). Our results revealed the variation in migratory tendency between different populations of crested ibis. Based on the distribution maps, it could be inferred that the northern populations would migrate southward to the Korean Peninsula from the Russian Far East and Northeast China for overwintering, since it would be counterintuitive to expect other populations migrated northward to colder areas during winter. Furthermore, the niche equivalency test also suggested the migratory behaviour in this subpopulation, whereas other conspecifics seemed to be year-round residents or partially migratory because of the wintering occurrences in south Japan and Taiwan. For many bird populations, only a proportion of the population migrates while others remain in the breeding

area year-round (Newton 2008), including some species related to crested ibis such as the Australian white ibis (*Threskiornis moluccus*) (Chan 2001) and roseate spoonbill (*Platalea ajaja*) (Degraaf and Rappole 1995). On the other hand, changing from sedentary to migratory behaviour has been found in some species when they expand their breeding ranges into higher latitudes (Maddock and Geering 1994; Rappole 2005). The migratory behaviour in crested ibis was eliminated probably due to severe range contractions. As the remnant resident population recover in the future, migratory behaviour may re-emerge with expansion to re-occupy its former range or colonize new areas (Newton 2008).

The SDMs have previously been used to relate the seasonal movements of migrating birds to a potential niche-tracking (or niche-switching) strategy based on the extensive (or little) overlap in environmental space between breeding and non-breeding niches (e.g., Marini et al. 2010; Marini et al. 2013). However, Laube et al. (2015) suggested that conclusion should not be drawn without considering the availability of environmental niche conditions in space and time and without evaluating the niche dynamics of alternative movement strategies. In our study, the equivalency and similarity of climatic niches between seasons indicated that the crested ibis was likely to utilise a particular set of climatic conditions year-round, as opposed to changing from one to another. More importantly, the seasonal niche overlap resulting from the observed migration pattern was higher than the one resulting from alternative hypothetical resident strategies, indicating that crested ibis compensated for the costs of a migratory journey by closely tracking its preferred climatic niche. These results may suggest that climatic niche tracking could be a main driver of migration in crested ibis. Our study provided an independent assessment of the migratory behaviour of the crested ibis and obtained more information than the speculative conclusions derived from limited field data.

5.4.3 Knowing the past to predict the future

The niche similarity test showed that crested ibis in the past and present shared more characteristics of the environmental niche spaces than randomly expected, which implies that the species had similar environmental constraints but a different set of variables within this environmental niche space restricted its distribution (Aguirre-Gutiérrez et al. 2015). This could also be supported by the finding of variations in the main environmental determinants and ecological responses of the models

calibrated in two periods. However, the non-equivalence of ecological niches among different time frames still implies a change in the species realized niches through time (Maiorano et al. 2013). Therefore, hindcasting or forecasting based on current data alone would not be accurate in such cases.

Climate change is expected to result in climatic zones moving poleward and an associated shift in the geographical ranges of bird species, and mounting evidence for such shifts has been found in European and North American birds (e.g., Auer and King 2014; Gillings et al. 2015). Our results revealed that the potential distribution of the crested ibis might also encounter a northward shift. The centre of the predicted wintering areas was predicted to shift in a northeasterly direction, in a similar manner to the range shift predicted for the black-faced spoonbill endemic to East Asia (Hu et al. 2010). With the northward expansion of the potential breeding areas, range contraction would be expected in the Northeast China and Russian Far East compared with the historical baseline range. More interestingly, the potential breeding habitat would also be expected to expand into Northwest China, where no occurrence has been documented in the past.

For the suitable areas occupied by the crested ibis at the present, conservation management could focus on the protection and restoration of the habitat at finer scales. With reintroduction programmes being carried out successively, crested ibis are no longer confined within one region or one country. Conservation of this species is thus an international problem and requires initiatives across a large geographic scale. The potential suitable areas that have not been occupied provide evidence could be used to select reintroduction sites. As the birds are currently sedentary and prefer similar environmental conditions year-round, selection of reintroduction sites must take geographical proximity of seasonal niches into account, and therefore areas suitable in both breeding and wintering seasons are prioritized.

Appendix

Table A5.1 Evaluation of crested ibis distribution models by the area under the receiver operating characteristic curve (AUC) (Mean $\pm$ SD) for breeding and wintering seasons during the historical and modern periods.

Model	Historical				Modern			
	Breeding		Wintering		Breeding		Wintering	
ANN	0.82	0.03	0.80	0.02	0.79	0.02	0.81	0.03
CAT	0.78	0.03	0.81	0.03	0.80	0.02	0.79	0.02
FDA	0.86	0.02	0.82	0.03	0.84	0.03	0.90	0.02
GAM	0.80	0.03	0.85	0.02	0.82	0.02	0.87	0.01
GBM	0.94	0.02	0.92	0.01	0.92	0.01	0.95	0.01
GLM	0.85	0.02	0.83	0.03	0.85	0.03	0.86	0.02
MARS	0.89	0.01	0.90	0.02	0.85	0.01	0.88	0.03
MaxEnt	0.95	0.00	0.94	0.01	0.96	0.00	0.97	0.01
RF	0.96	0.01	0.96	0.01	0.94	0.00	0.98	0.00

ANN, artificial neural networks; CTA, classification tree analysis; FDA, flexible discriminant analysis; GAM, generalized additive models; GBM, generalized boosting models; GLM, generalized linear models; MARS, multivariate adaptive regression splines; MaxEnt, maximum entropy; RF, random forests.

Chapter 6

Synthesis: Spatial Ecology for Conservation of Crested Ibis

6 Synthesis: Spatial ecology for conservation of crested ibis

6.1 Introduction

Many species have suffered severe decline and range contraction and become threatened with extinction due to the ongoing threats from habitat loss and anthropogenic disturbance (IUCN 2007; Deinet et al. 2013). Effective conservation of species requires adequate knowledge of species' natural habitat and how individuals interact with it. Understanding species-environment relationships requires recognition of the complexity of factors in biotic and abiotic environment responsible for creating the spatial patterns in species distributions, and the relationships should be observed and analysed with the context of geography and history. Empirical research that emphasizes responses of species to spatially-structured habitats has shown a useful link between conservation biological research to practical mechanisms for conservation and restoration planning (Collinge 2001). Taking the crested ibis as the focal species, the main goal of this thesis is to investigate and gain insight into the spatial response of this endangered but recovering species to a changing human-dominated landscape, with advanced applications of remote sensing, GIS, geospatial analysis and predictive modelling techniques.

In this thesis, several studies framed around the patterns and processes of landscape change, and species-environment relationships at multiple scales in space and time are presented. Albeit with some overlap, these studies can be classified into four overarching themes: (1) critical habitat mapping and monitoring (Chapter 2 & 3); (2) spatial and temporal variation in species-environment relationships (Chapter 3 & 5); (3) species range dynamics in a heterogeneous landscape (Chapter 4); (4) spatial response of species under environmental change (Chapter 5). In this final chapter, the major research findings from previous chapters are highlighted and brought together to understand crested ibis and its relationship with environment in a dynamic landscape from a spatial-ecological perspective. The practical relevance of these results to the development and implementation of conservation strategies for crested ibis is discussed.

6.2 Current range of the crested ibis

In May 1981, after three years of a nation-wide survey, a tiny wild population of seven birds (two pairs and three fledglings) was rediscovered in Yang County, Shaanxi Province in Central China. Thanks to an intensive conservation effort during the last 30 years, the distribution of wild crested ibis population has expanded to more than ten counties (Fig. 6.1b), such as Chenggu, Xixiang and Ningshan, around Yang County. Field survey showed that, at present, more than 95% of the population still inhabits within Yang County (Wang et al. 2014). With the development of captive populations, several reintroduction attempts have been made to establish new populations in Ningshan and Tongchuan of Shaanxi Province, Dongzhai National Nature Reserve in Henan Province, Xiazhuhu National Wetland Park in Zhejiang Province (Fig. 6.1a). Meanwhile, captive-bred birds have been released into wild on Sado Island in Japan since 2008, with further reintroductions subsequently.

Figure 6.1 a. Current distribution of the crested ibis, including one wild population and several reintroduced populations. **b.** The wild population has expanded its range to nearby counties of Yang County.

6.3 Understanding the natural history of crested ibis - What is the baseline of geographical and ecological distributions of crested ibis?

A better understanding of species distribution and its environmental requirements in the past prior to widespread human disturbance is essential to inform us about the current state of the species and its potential response

to future environmental change. For many species, knowledge of their historical distributions may be as superficial as a few names of locations where the species has been observed, or oversimplified range maps outlined based on written records. These data present a far-from-complete picture of species distribution, being insufficient in spatial accuracy for proper scientific analyses and conservation planning. In Chapter 5, species distribution modelling based on extinct population records as well as historical climate and land use data was used to establish the baseline of geographical distribution of the crested ibis at a broad scale. The modelled historical distribution of the crested ibis exhibit a much larger range than today, and the pattern is generally consistent with the historical range described in the literature, specifically that the crested ibis bred in the Russian Far East, Japan and mainland China, and visited the Korean Peninsula and Taiwan in winter (Fig. 6.2). The predictions provide a more precise depiction of crested ibis distributions during the breeding and wintering seasons, and help to eliminate controversy around the historical distribution due to the lack of observation records.

As for the ambiguous migratory tendency of crested ibis, it could be inferred from the seasonal distribution maps that the northern populations would migrate southward to the Korean Peninsula from the Russian Far East and Northeast China for overwintering, since it would be counterintuitive to expect other populations migrated northward to colder areas during winter. The quantification and testing of niche similarity between seasons also suggest that the crested ibis was partially migratory in the past. Furthermore, the crested ibis was likely to utilise a particular set of climatic conditions in seasonal movements, implying that climatic niche tracking could be a main driver of migration in crested ibis.

The use of historical information provides a more robust assessment of species distributions in geographical and ecological space, and obtains more reliable information than the speculative conclusions derived from limited field data.

Figure 6.2 Historical baseline of geographical distribution of crested ibis in the breeding season (a) and wintering season (b). The colour chart represents species occurrence probability in a grid cell above the threshold maximizing the sum of sensitivity and specificity, from low (light yellow) to high (dark brown).

6.4 Mapping and monitoring the critical habitat for crested ibis - Has the traditional rice farming been effectively maintained?

Winter-flooded rice farming is a traditional agricultural practice that involves single cropping and then flooding the fallow field during winter to ensure an adequate water supply for the next year. Conservation scientists and practitioners have widely recognized that the flooded rice fields provide alternative or complementary foraging habitats for waterbirds during the winter and breeding seasons (Elphick 2000; Wood et al. 2010; Toral et al. 2011). The winter-flooded rice fields in the Qinling Mountains, China, are the last refuge for the endangered crested ibis. Considerable efforts have been made to protect this anthropogenic habitat since the discovery of the relict crested ibis population in 1981, focusing on maintaining the traditional practice of winter-flooding and compensating the farmers for their consequent loss of income. The consequent conflicts between the agricultural and conservation communities raise the question as to whether the traditional rice farming has been effectively maintained.

In Chapter 2, analyses of multi-temporal satellite data and ancillary topographic data were performed to monitor the spatio-temporal change of winter-flooded rice fields from 1988 to 2001, and to 2009. Integrated remote sensing and GIS techniques yielded precise spatial information on the distribution of scattered winter-flooded rice fields in the mountainous topography, with an overall accuracy >89% and a Kappa statistic >0.87 for all three time frames. The results show that winter-flooded rice fields have been continuously reduced across the current range of crested ibis from 1988 to 2009, with a much higher annual loss rate during 2001-2009 (5.5%) compared to the rate during 1988-2001 (0.4%). Unexpectedly, the rate of loss of these fields in the core-protected areas has increased to a higher level than that in non-protected areas between 2001 and 2009 (Fig. 6.3). Large proportions of the lost winter-flooded rice fields were converted to other arable land as well as shrub/grass, but different patterns of land-use conversion were found in the core-protected areas and non-protected areas. Demographic and socio-economic pressures as well as national policies were likely responsible for the reduction of winter-flooded rice fields in the core-protected areas.

The mechanism for the population growth of crested ibis under the change of winter-flooded rice fields was also investigated using a numerical response model. The results indicate that a reduction of winter-flooded rice fields decreases the population growth of crested ibis, and the population growth in this area will be constrained by the continuous decline of traditional winter-flooded rice fields in the coming decades.

Figure 6.3 Land cover/use maps in protected (Areas 1 and 2) and non-protected (Area 3) areas for the years 1988, 2001 and 2009. The acreage of the winter-flooded rice fields in each area is indicated by the position of the center of the circle. The annual rate of change for each period in each area is given below the lines.

6.5 Assessing species-environment relationships at multiple scales in space and time - Is there spatial and temporal variation in species-environment relationship? Can this be estimated using field observation?

The geographical distribution of a species depends on a wide variety of biotic, abiotic and historical processes operating at different spatial and temporal scales (Guisan and Thuiller 2005). Relationships between species and environment are not always constant (Lunghi et al. 2015). Individuals may prefer different environments in different periods, or be forced to change to adapt the changing environment (Nogués-Bravo 2009; Stigall 2012; Brambilla and Saporetto 2014; Lunghi et al. 2015).

Climatic variables have been considered the main drivers of broad-scale diversity patterns (Hawkins et al. 2003). In Chapter 5, we examined the climatic niche stability for crested ibis from the past to present. An ordination technique was used, allowing for direct comparisons of species-environment relationships in environmental space (Broennimann et al. 2012). The niche similarity test show that crested ibis in the past and present shared more characteristics of the climatic niche space than randomly expected (Table 6.1). However, the niche equivalency test show that the climatic niches of the crested ibis occupied in the past and present were not interchangeable, which implies a change in the species realized niches through time (Maiorano et al. 2013). Moreover, broad-scale species-environment relationships were also investigated based on species distribution models. Variations were found in the main environmental determinants and ecological responses of the models calibrated in two periods, which may support that the species had similar environmental constraints but a different set of variables within this environmental niche space restricted its distribution (Aguirre-Gutiérrez et al. 2015).

Table 6.1 The overlap, similarity and equivalency of climatic niches occupied by crested ibis from the past to present.

Season	Period		Niche overlap (D)	Niche similarity		Niche equivalency
	a	b		a→b	b→a	
Breeding	Historical	Modern	0.49	similar*	ns	non-equivalent*
Wintering	Historical	Modern	0.52	similar*	similar*	non-equivalent*

*statistically significant ($p < 0.05$)

ns, not significantly different

As for the local scale, previous studies suggested that the distribution of winter-flooded rice fields plays an essential role in nest site selection by the crested ibis in the initial stage of population recovery (Wang, Zhao, et al. 2000; Li et al. 2001; Ding 2004; Zhang et al. 2008). As the relict crested ibis population is increasing in size and expanding its geographical range, the species may exhibit different response to the habitat (Gonzalez et al. 2008). In Chapter 3, we quantified the spatial relationships between the nest site clusters and winter-flooded rice fields (based on the satellite-derived distribution map obtained in Chapter 2) using clustering method and point pattern analysis. The results show that both have significantly clumped distribution patterns and that they are positively associated as a whole. However, the dependence of crested ibis on the winter-flooded rice fields varied significantly among the nest site clusters, and has decreased over the years (Figs. 6.4 and 6.5), as the recently expanding population shows a return to more varied habitats. The changing role of winter-flooded rice fields in nest site selection by the crested ibis may suggest the behavioural plasticity and an adaptive response to a heterogeneous environment, which allow the birds to balance limitations experienced in the available habitats (Treinys et al. 2008; Jia et al. 2013).

Figure 6.4 Spatial association between nest sites and winter-flooded rice fields in the nest site clusters. Bivariate L-function $L_{12}(r)$ against distance r for each cluster is plotted (A-E). Solid lines are observed values of $L_{12}(r)$. Dotted and dashed lines are the theoretical values and the 95% confidence envelopes, respectively, for the pattern expected under the null hypothesis of population independence. Values of $L_{12}(r)$ above the upper envelope indicate a significant positive association, whereas values of $L_{12}(r)$ below the lower envelope indicate a significant negative association. The year when the nest site was first established in the cluster is given.

Figure 6.5 Variations in the spatial association between nest sites and winter-flooded rice fields over the years. Observed L-function values from bivariate L-function analysis for the five nest site clusters (A-E) established over the years are shown by box plots. A positive value indicates a spatial aggregation between two populations of points and a negative value indicates a spatial segregation between them. The only pair with no significant difference is annotated based on post-hoc pairwise Tukey's HSD test ($p \geq 0.05$).

We have demonstrated remote sensing and GIS techniques are effective for habitat mapping and modelling at a landscape scale. These spatially continuous, streams of habitat data are not, however, likely to be collected by ground surveys alone. Species-environment relationships can be estimated by field observation only at a local scale. Ecologists will confront more challenges when it comes to large areas or areas with difficult access. When upscaling the species-environment relationship in space and time, especially for a continental scale and a historical period, it is no longer

feasible to count on field observation. With advanced applications of remote sensing, GIS, geospatial analysis and predictive modelling, investigation and monitoring of the distribution of species and its habitat can increase the understanding of species-environment relationships over space and time. Given the spatial and temporal variation in species-environment relationship, this study supports the view that caution should be exercised when interpreting the ecological requirements of species based on its current distribution, especially when the distribution is narrow (Gonzalez et al. 2008; Wang and Li 2008). The deviation from the niche stability assumption may limit the model predictive performance and model transferability in time, resulting in improper or inadequate conservation assessments and plans for species.

6.6 Modelling species rang expansion in a heterogeneous landscape - What factors limit and regulate the range dynamics of crested ibis?

With conservation efforts focused on legal protection, habitat management and restoration as well as species reintroductions, some threatened bird species have now been recovering after a period of serious declines (Deinet et al. 2013). Understanding and predicting spatio-temporal recolonization of these species in a heterogeneous landscape are imperative for their conservation planning. By using static spatial predictions from SDMs in spatially explicit simulations of non-equilibrium population dynamics, hybrid modelling substantially improves our ability to predict species range expansion and understand processes affecting the dynamics (Franklin 2010).

In Chapter 4, we first used a presence-only species distribution model to predict breeding habitat suitability for crested ibis based on satellite-derive vegetation and water indices as well as bioclimatic variables, and then integrated the habitat suitability map into a spatially explicit and individual-based dynamic modelling platform to simulate the range dynamics of crested ibis. Assuming unchanging environmental conditions, life-history traits and protection status as well as no catastrophic diseases, the crested ibis population is predicted to continue to increase in size, expand its geographical range and recolonize some part of its former range in the next 50 years. However, the majority of the population will still be restricted to a relatively small range, and some potential suitable habitat seems very unlikely to be recolonized by natural dispersal in decades.

Table 6.2 Sensitivity of range dynamic model outputs based on 243 combinations of uncertain parameters, strength of density dependence ($1/b$), probability of short-distance dispersal events (P), subadult survival probability (S_s) and adult survival probability (S_a) (direction of impact shown in parentheses).

Output	Year	Explained variance by parameter uncertainty (%)			
		$1/b$ (+)	P (-)	S_s (+)	S_a (+)
Male population size	2020	38.1	ns*	26.0	34.4
	2040	28.0	2.41	25.6	39.8
	2060	20.9	13.5	21.9	30.5
No. of occupied cells	2020	40.6	ns*	26.5	32.5
	2040	26.0	7.81	24.6	35.8
	2060	19.7	20.5	21.2	28.0
Range extent (km ²)	2020	9.23	58.0	5.57	7.14
	2040	9.74	47.4	8.97	14.5
	2060	10.6	31.0	10.7	17.1

* ns, no significant contribution of the parameter to variation in predictions

Understanding the factors that limit species range expansion, especially those controllable or affected by management actions, is crucially important in building effective management and conservation strategies (Marcot et al. 2015). We therefore assessed the impacts of uncertainty in demographic and dispersal parameters on the simulation of range dynamics. The results indicate that the simulated range dynamics is sensitive to species' life-history trait parameters to varying degrees and temporal scales (Table 6.2). Adult, and to a lesser extent subadult, survival probability show a substantial influence on the predicted demographics of crested ibis. In addition, the considerable sensitivity to uncertainty in the strength of density dependence (a principal determinant of carrying capacity in our study), especially when the majority of the crested ibis population is still restricted to the local range, may imply that decreasing habitat suitability and availability could have a negative effect on range expansion of crested ibis. Earlier studies have demonstrated that long-distance dispersal may contribute to species persistence in fragmented landscapes (Tittler et al. 2006). The results of this study show that the proportion of long-distance

dispersal events shows the strongest effect on the geographical feature of the range dynamics. A greater probability of long-distance dispersal events could result in a faster and further range expansion of crested ibis.

6.7 Predicting species distribution under environmental change - Will projected climate and land-use changes impact the potential distribution of crested ibis?

Global climate and land-use changes are of major scientific and political concern, especially when considering their potential impacts on future biodiversity (Thomas et al. 2004; Foley et al. 2005; Lawler 2009). Forecasted changes in climatic conditions imply that the distribution of a species will shift if it is able to spatially track shifting climatic conditions (Barbet-Massin, Thuiller, et al. 2012). Land-use change is also expected to have significant effects for terrestrial ecosystems (Sala et al. 2000), especially for birds (Lee and Jetz 2011). Geospatial analyses can be utilized to forecast the directionality and magnitude of shifting habitats and thus be deployed for predicting the future distribution of biodiversity. In Chapter 5, SDMs with an ensemble forecasting framework were combined with scenarios of future environmental change to provide a general insight into the future potential distribution of crested ibis. Future scenarios were projected based on the implementations of Representative Concentration Pathways, the most advanced simulations available of global climate system response to changes in radiative forcings as well as different combinations of economic, technological, demographic, policy, and institutional futures (Moss et al. 2010).

The results of this study reveal that the potential distribution of the crested ibis may encounter a northward shift (Fig. 6.6). As climate change may result in climatic zones moving poleward, an associated shift in the geographical ranges of bird species can be expected, and mounting evidence for such shifts has been found in European and North American birds (e.g., Auer and King 2014; Gillings et al. 2015). Compared with the present range, the potential breeding distribution is projected to shift 570 km northward, and the potential wintering distribution shift 939 km to the northeast. The results also show that the potential suitable areas for crested ibis are expected to shrink in both breeding and wintering ranges compared

to historical baselines (by 30% and 18% in the 2080s, respectively). In addition, habitat in Central China for both seasons, where the crested ibis is occupying currently, would become less suitable in the future (Fig. 6.6).

Figure 6.6 Predicted suitable areas for the crested ibis during breeding (a, c) and wintering (b, d) seasons in the present (a, b) and future (c, d) under climate and land-use change. The colour chart represents the probabilistic niche suitability in a grid cell above the threshold maximizing the sum of sensitivity and specificity, from low (light yellow) to high (dark brown).

6.8 Relevance to conservation and management

Geographical information on the distribution of wildlife and its habitat forms a fundamental source of information in conservation management. With the advanced applications of remote sensing, GIS, geospatial analysis

and predictive modelling, this thesis has demonstrated a spatial-ecological perspective in understanding the response of crested ibis to a changing human-dominated landscape. The findings presented in this thesis enable prioritization of conservation efforts, and provide timely and accurate information for conservation biologists and governing authorities to implement proactive strategies for *in-situ* conservation and reintroduction of crested ibis.

China's wildlife conservation legislation and increasing public awareness have greatly reduced anthropogenic disturbances and almost eliminated the risk of human-induced mortality (due to hunting and poisoning). The crested ibis is predicted to continue to increase in size, but the majority of the population will still be restricted to a relatively small range. Some potential suitable habitat seems very unlikely to be recolonized naturally by crested ibis, at least in the next few decades. The species might still be at substantial risk from catastrophic changes (e.g., habitat loss, diseases and climate disasters) in Shaanxi. To reduce the risk of a catastrophe to the single population of crested ibis, reintroduction programmes have been carried out for several years both in China and Japan (Yamagishi 2009; Yu et al. 2009). Our study suggests that reintroductions near the current crested ibis range (within a maximum dispersal distance of crested ibis) have a positive effect on crested ibis range expansion. Current reintroduction programmes in Shaanxi are expected to speed up the recolonization of the historical range and facilitate the establishment of satellite populations.

With population expansion and reintroduction programmes being carried out successively, crested ibis are no longer confined within one region or one country. Conservation of this species is thus an international problem and requires initiatives across a large geographic scale. The historical data provide a baseline for conservation and restoration. Areas with similar ecological characteristics could be occupied again if the crested ibis has kept its adaptive ability to this niche. The potential distribution of crested ibis provides scientific evidence to guide the selection of reintroduction sites and underpin the designation of protected areas. As the birds are currently sedentary and prefer similar environmental conditions year-round, selection of reintroduction sites must take geographical proximity of seasonal niches into account, and therefore areas suitable in both breeding and wintering seasons are prioritized. Considering the future climate change, areas with both current suitable climate and future suitable climate can be prioritized. For suitable areas predicted at a broad scale,

conservation management should also focus on the protection and restoration of the habitat at finer scales.

Traditional rice production provided essential habitats for the survival and reproduction of crested ibis during the early stage of the relict population recovery, and still has a positive influence on its conservation. It is advocated that some patches of winter-flooded rice fields should be uniformly maintained, especially in areas with less natural and semi-natural wetland. The protection will not achieve the desired outcome simply by forcing the farmers to participate in conservation efforts, which may further aggravate the conflicts between conservation and local communities.

Two national policy programs, China's Western Development policy launched in 2000, and the new socialist countryside construction (Rogers and Wang 2006; Li et al. 2011), have changed both economic and lifestyle activities of local residents in the remote mountains. More and more labour force and farmers have given up their farming income and become migrant workers in the cities (Duan et al. 2013; Sai et al. 2013). To alleviate poverty and sustainably manage the ecosystem, local residents are also being relocated from their remote mountain homes, which have been deemed unsuitable for sustaining human life, to regions with better economic prospects. Labour migration and urbanization may reduce the use of agrochemicals and fuel wood and thereby reduce environmental stress (Duan et al. 2013), which is beneficial to the recovery of crested ibis population. However, these changes may result in more arable land, especially winter-flooded rice fields, being abandoned. In addition, China's Grain for Green Program (Liu et al. 2008), to return steep slopes of cultivated land to forest and grassland, will also contribute to the continuous loss of winter-flooded rice fields in the future.

Maintenance and restoration of winter-flooded rice fields require the understanding and cooperation of local residents with the promotion of reforms to organic and ecological farming practices (Su 2008). Legislation may need to propose incentives for biodiversity-friendly and lower-impact farming practice, thereby trying to eliminate the threats of agricultural intensification and abandonment. Supporting or mimicking traditional agriculture is a conservation paradigm in Europe and other developed countries (Wright et al. 2012). For instance, the Kabukuri wetlands and the surrounding winter-flooded rice fields in the Miyagi Prefecture of Northeast Japan (Tōhoku region) is an initiative of wetland restoration by

promoting environmentally-sound agricultural practices, and a pioneer of payments for ecosystem services in agriculture in Japan (Kurechi 2007). These winter-flooded rice fields have been registered as protected wetlands under the Ramsar Convention in 2005, contributing to a population increase of migratory geese (Amano 2009). Learning from this initiative, human-made wetland habitat restoration has been implemented for conservation of reintroduced crested ibis by incorporating agri-environmental schemes in Sado Island since 2008 (Nakamura et al. 2014).

Meanwhile, efforts should be made to restore the functionality of the natural and semi-natural wetland habitat, since it becomes more important to the survival of crested ibis when it returns to more varied habitat in the human-dominated Han River floodplain. The Han River is the water source of the central route of the South–North Water Transfer Project in China (Ye et al. 2014). Recently, catchment protection policies have been implemented to protect the quality of water supply (Pohlner 2015), which have the potential to facilitate the restoration of wetland habitat for crested ibis.

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Summary

Many species have suffered severe decline and range contraction and become threatened with extinction due to ongoing threats from habitat loss and anthropogenic disturbance. The Asian crested ibis (*Nipponia nippon*) was originally widespread in East Asia, but the population declined severely in the mid-twentieth century, leading to extirpations throughout almost all of its former range. Considerable efforts have been made to protect the relict population and core habitat in the Qinling Mountains, China. Currently, the crested ibis population is increasing in size and expanding its geographical range. However, knowledge about this species and its habitat is still limited for landscape-scale conservation. Developing a comprehensive conservation strategy requires a simultaneous understanding of patterns and processes of landscape change as well as detailed responses of species to these modifications over geographical space and time.

The main goal of this thesis is to investigate and gain insight into the spatial response of this endangered but recovering species to a changing human-dominated landscape, with advanced applications of remote sensing, geographical information system, geospatial analysis and predictive modelling techniques.

The results presented in this thesis show that the traditional winter-flooded rice fields have been continuously reduced across the current range of crested ibis even under protection, which is likely to pose a threat to the population recovery of crested ibis in the local area. The dependence of breeding crested ibis on the winter-flooded rice fields varies spatially and decreases over the years, with the recent return of crested ibis to more varied habitats. Given the current strict conservation combined with higher public awareness, the crested ibis population is expected to continue to increase in size and expand its range, and recolonize parts of the former range. Among the life-history trait parameters that affect the range dynamics of crested ibis, adult survival probability and the proportion of long-distance dispersal events show the strongest effects. The use of historical data indicates that the crested ibis seems to occupy similar niches between seasons and over time. In the face of future climate and land-use changes, the potential suitable areas for crested ibis are expected to shrink

and shift northward. These findings enable prioritization of conservation efforts, and provide timely and accurate information for conservation biologists and governing authorities to implement proactive strategies for *in-situ* conservation and reintroduction of crested ibis.

Samenvatting

De populatie van veel diersoorten is afgenomen in aantallen en spreiding. Dit is mede door het afnemen van hun leefruimte en de antropogene verstoring. Oorspronkelijk was de Aziatische kuifibis (*Nipponia nippon*) wijdverbreid in Oost-Azië, maar de populatie daalde sterk in het midden van de twintigste eeuw door de uitroeiing van bijna de gehele omvang. Er zijn toen aanzienlijke inspanningen gedaan om de nog bestaande soorten en hun leefruimte, in het Qinling-gebergte in China, te beschermen. De populatie van de kuifibis is inmiddels weer aan het toenemen in aantallen en verspreiding over de leefruimten.

Kennis van de Aziatische kuifibis is echter nog steeds te beperkt voor het behoud op landschap-schaal. Het ontwikkelen van een alomvattende strategie voor het behoud vereist een gelijktijdige inzicht in patronen en processen van het veranderende landschap, evenals gedetailleerde kennis van de soorten om deze wijzigingen op het gebied van geografische ruimte en tijd te begrijpen.

Het belangrijkste doel van dit proefschrift is om te onderzoeken en inzicht te krijgen in de ruimtelijke respons van deze bedreigde, maar herstellende diersoorten in een veranderende, menselijke gedomineerde, landschap. Hierbij worden geavanceerde toepassingen gebruikt op gebied van remote sensing, geografisch informatiesystemen, geospatiale analyse en voorspellende modellerende technieken.

De resultaten in dit proefschrift laten zien dat het aantal ondergelopen rijstvelden in wintertijd in de afgelopen jaren voortdurend afgenomen is. Dit kan in deze omgeving een bedreiging zijn voor de kuifibis die zich juist voorplanten in deze rijstvelden in de winter. De kuifibis worden hierom ook steeds meer gesignaleerd in andere type leefruimte. Door het huidige strenge behoud in combinatie met hogere publieke bewustwording, zal de kuifibis herpopulatie naar verwachting blijven toenemen in omvang en zal zich herkoloniseren. De dynamische omvang- en spreiding van de kuifibis is afhankelijk van de historische levens-eigenschappen van het dier, maar ook de overlevingskansen en de lange afstands-spreiding is van grote invloed. Uit historische gegevens blijkt dat de kuifibis vergelijkbare niches gebruikt over tijd en tussen de seizoenen door. In het licht van de toekomstige klimaat- en landgebruik veranderingen, zullen de potentieel

geschikte gebieden voor de kuifibis afnemen en geleidelijk meer verschuiven in noordelijke richting.

Met deze bevindingen is het mogelijk om prioriteiten te stellen voor pogingen tot de instandhouding van de soort. Ook kan tijdige en accurate informatie gebruikt worden door biologen en bestuurlijke autoriteiten om zo proactieve strategieën te ontwikkelen voor het behoud en de herpopulatie van de kuifibis in zijn oorspronkelijke leefruimte.

Biography

Yiwen Sun was born on June 1, 1987 in Hubei, China. In 2009 she obtained BSc degree in Geo-information Science from Wuhan University, China, and was recommended for admission to be a postgraduate without examination. She then enrolled in a joint masters degree program between Wuhan University and Faculty ITC of University of Twente in the Netherlands. She received her MSc degrees in Geo-information Science and Earth Observation from University of Twente as well as in Cartography and Geo-information Engineering from Wuhan University in 2011. In the same year, she was awarded a four-year doctoral scholarship from the China Scholarship Council and began her PhD research in Spatial Ecology at the Natural Resources Department of ITC.

Since 2016, Yiwen has served as a researcher at ITC, working on a European Space Agency (ESA) sponsored project: GlobWetland Africa. Her overall research interest lies in remote sensing of land use and land cover, ecological modelling, spatial ecology, global change ecology, and biodiversity conservation.

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