



Predicting and understanding spatio-temporal dynamics of species recovery: implications for Asian crested ibis *Nipponia nippon* conservation in China

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ABSTRACT

Aim 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 to guide its *in situ* conservation and plan possible reintroductions.

Location Central China.

Methods 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.

Results 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.

Main conclusions 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.

Keywords

dispersal, habitat suitability, range expansion, spatially explicit individual-based model, species recovery, threatened species.

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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 & McIntire, 2010). The accurate prediction of potential habitat and species range dynamics is therefore imperative to plan the recovery of target species.

Historically, Asian crested ibis *Nipponia nippon* (hereinafter referred to as 'crested ibis') 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 ongoing 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 & 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 hybridization 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; Bocedi *et al.*, 2014b). 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 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 parameterization, 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.

METHODS

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. 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.

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 $n = 100$).

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 S1 and Table S1).

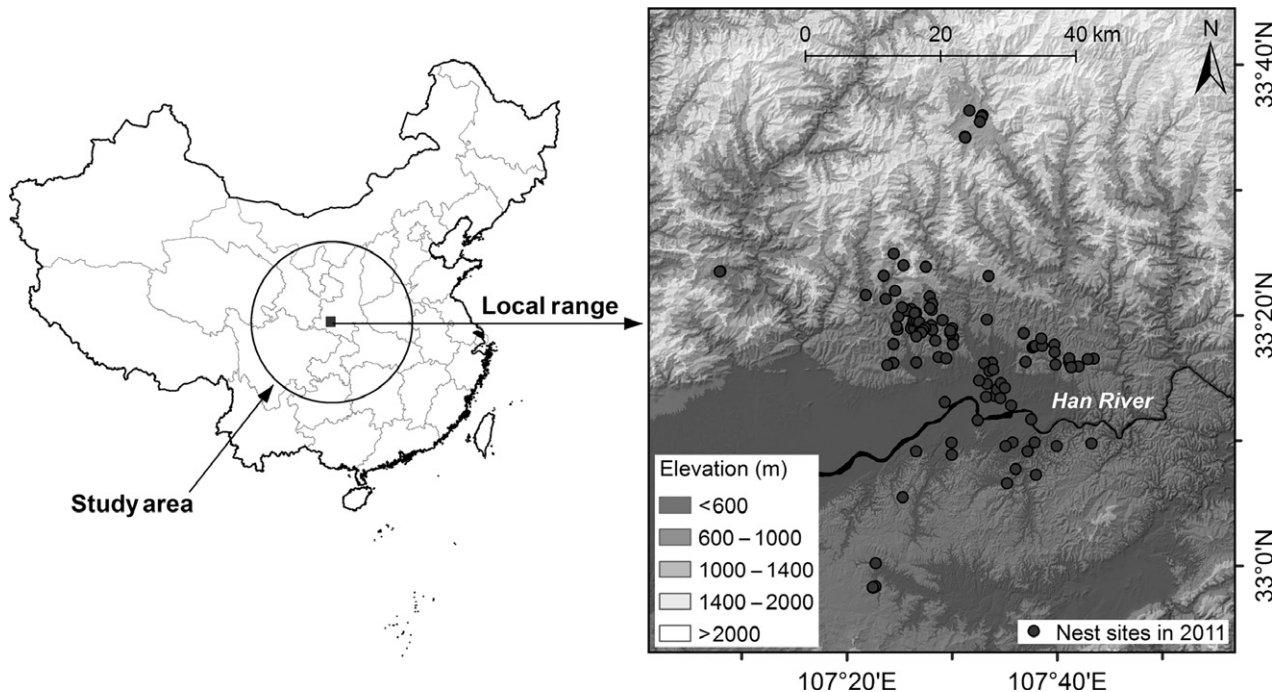


Figure 1 Map of the study area and the current range (local range) of breeding crested ibis in China. The locations of nest sites in 2011 are marked with black dots.

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, 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 S1 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.

Range expansion modelling

Range expansion modelling was conducted using RANGESHIFTER v1.1, a platform for spatially explicit, individual-based modelling of species range dynamics (Bocedi *et al.*, 2014b), which integrates population dynamics and dispersal models. The cell-based model ran over the habitat suitability map reprocessed for range expansion modelling (see Appendix S1 for details). 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 & 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 (Bocedi *et al.*, 2014b). The model included three-stage classes: juveniles (< 1 year), subadults (1–2 years) and adults (≥ 2 years). 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:

$$\begin{bmatrix} 0 & 0 & \Phi \\ 1.0 & 0 & 0 \\ 0 & S_s & S_a \end{bmatrix}$$

where S_s is subadult survival probability, S_a 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 & 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 (P_e) of 0.95, as 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 (D_s and D_l , respectively) and the probability of short-distance dispersal events (P). D_s was fixed at 5.9 km in accordance with field observations (Yu *et al.*, 2010), whereas D_l 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 initialization, calibration and validation

We used nest site localities in 1994 to initialize the species distribution and a quasi-equilibrium distribution to initialize 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 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 parameterization, calibration and validation are elaborated in Appendix S1.

Future range expansion predictions

We used nest site and population data from 2011 for initialization 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).

Table 1 The fixed and optimized RANGE-SHIFTER parameters set for range expansion modelling and their estimated bounds for sensitivity analysis based on the quality of information available (lighter grey representing better quality of information and consequently smaller parameter uncertainty).

Parameter (Unit)	Value	Description	Estimated range
MaxAge	16	Maximum age	–
Φ	2.0	Number of male offspring per male	–
P_e	0.95	Emigration probability of juveniles	–
D_s (km)	5.9	Mean distance of short-distance dispersal	–
P	0.95	Optimal probability of short-distance dispersal events	0.92–0.98
S_s	0.67	Optimal subadult survival probability	0.61–0.71
S_a	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
D_l (km)	30	Optimal mean distance of long-distance dispersal	27–33

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 , $1/b$, D_l 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 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.

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 S1 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.

RESULTS

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 S2). 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. 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 and 150 km, respectively, from the current crested ibis range.

Range expansion modelling with optimal parameters

The population trajectory predicted using the optimal parameters followed the observed population trend very well (see Fig. S1). The simulation of nest site distribution for year 2011 (see Fig. S2) 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. 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.

Impact 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 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

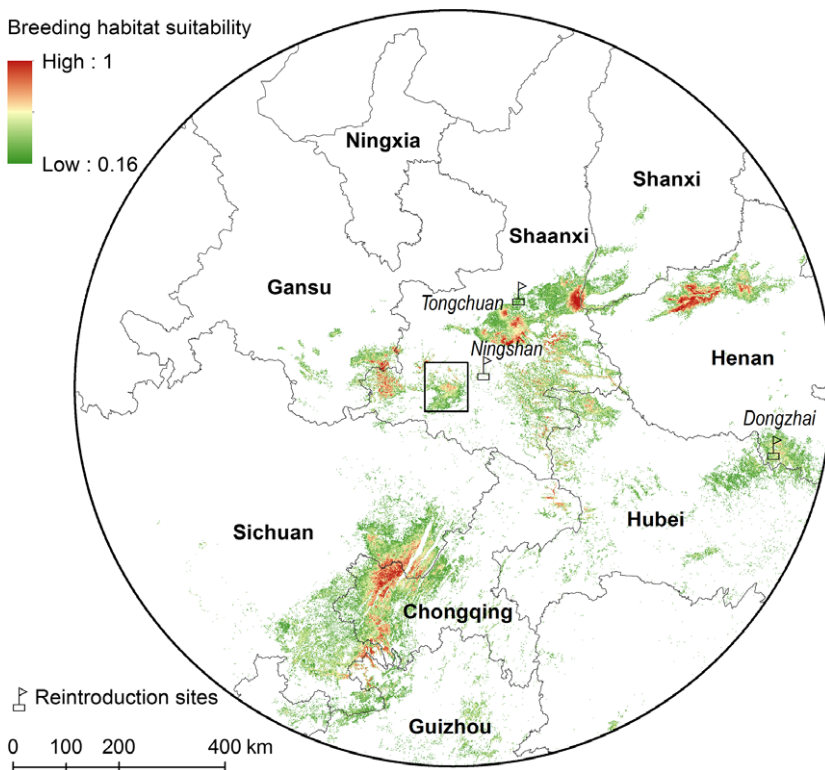


Figure 2 Predicted habitat suitability for breeding crested ibis from the MAXENT model. The area within the rectangle indicates the current range (local range) of breeding crested ibis. Three reintroduction sites are marked with flag symbols.

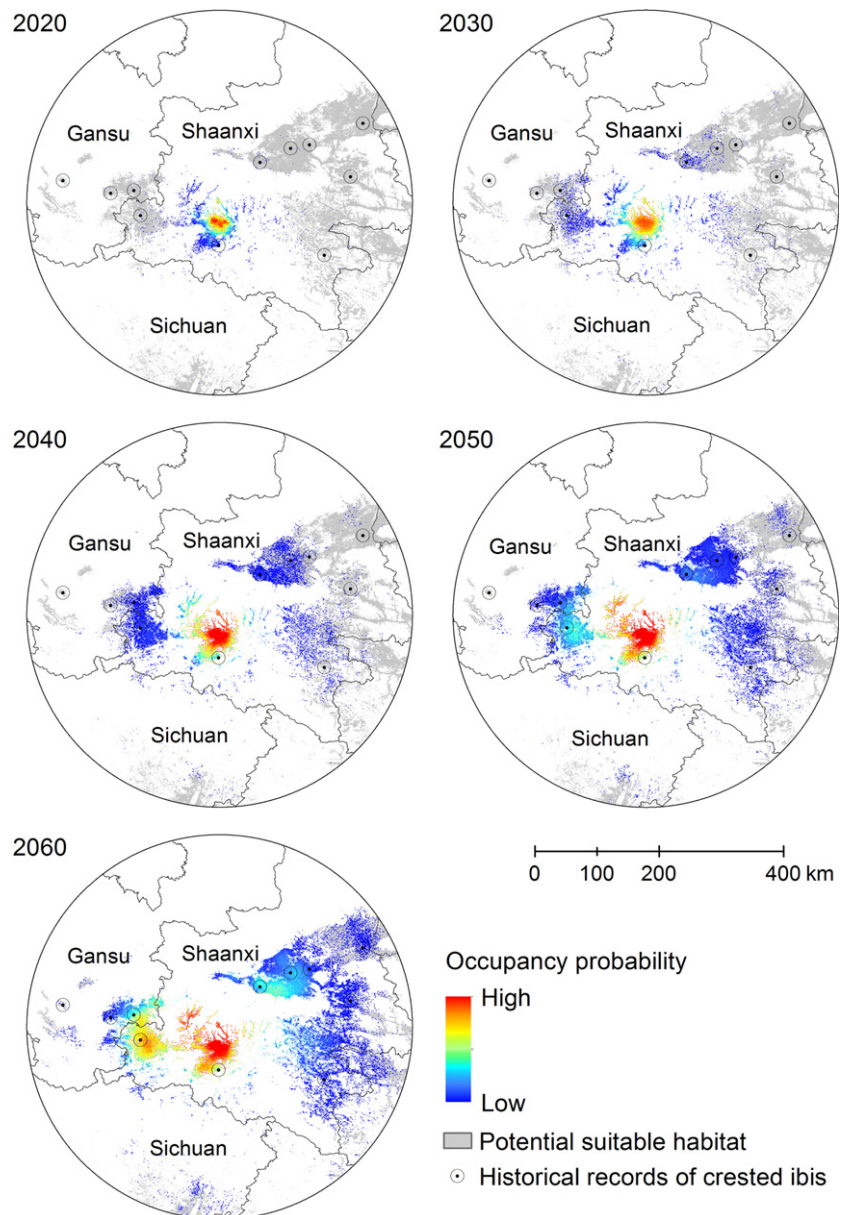


Figure 3 Predicted range expansion within 300 km of the current local range of breeding crested ibis in years 2020, 2030, 2040, 2050 and 2060. Occupancy probability of a cell was assessed based on 100 replicate simulations. The locations of principal historical records are marked with circled dots.

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. Dl 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).

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 S3). By 2060, mean population size, number of occupied cells and range extent were reduced by 40%, 34% and 16%, respectively, when local

Table 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 (DI), 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	Mean	SE	Explained variance by parameter uncertainty (%)				
				$1/b$ (+)	DI (+)	P (-)	S_s (+)	S_a (+)
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	14,740	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	25,400	454	9.23	12.7	58.0	5.57	7.14
	2030	53,000	1030	8.52	14.2	52.7	7.82	11.0
	2040	79,800	1560	9.74	14.1	47.4	8.97	14.5
	2050	110,000	2340	10.6	13.2	45.0	9.50	15.9
	2060	146,000	3200	10.6	12.2	31.0	10.7	17.1

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

extinction probability was 0.03, and by 58%, 52% and 29%, respectively, at 0.05 probability (see Table S3 for results from the alternative way of including stochastic extinction).

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 large catastrophes, 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. 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 (Bocedi *et al.*, 2014a; 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 RANGE-SHIFTER), 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 & McIntire, 2010). As shown for many species, habitat fragmentation and destruction can hamper their dispersal abilities (Collingham & 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 & 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

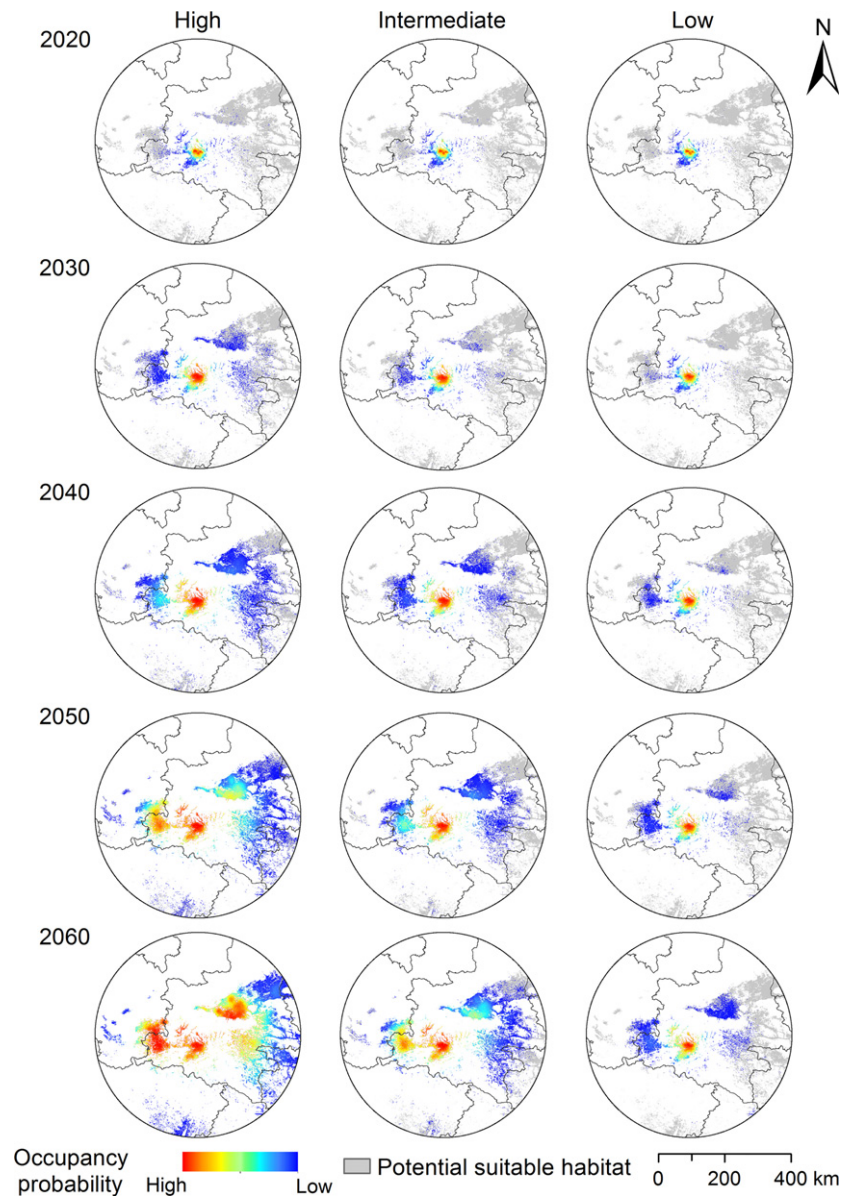


Figure 4 Uncertainty in the predicted range expansion within 300 km of the current local range of breeding crested ibis in years 2020, 2030, 2040, 2050 and 2060 due to parameter uncertainty. The selected high, intermediate and low scenarios of model configurations produced the fastest, medium and slowest recolonization by crested ibis, respectively. Occupancy probability of a cell was assessed based on 100 replicate simulations for each scenario.

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).

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 & 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 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.

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 parameterization 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. 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 interpatch 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. 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.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Methods.

Figure S1 Trajectories for observed and predicted populations.

Figure S2 Predicted nest site distribution of the crested ibis for year 2011.

Figure S3 Differences in model outputs between the original model and models including stochastic extinction.

Table S1 Description of environmental variables.

Table S2 Relative importance of environmental predictors of habitat suitability.

Table S3 Relative changes in model outputs of models including stochastic extinction compared with the original model.

BIOSKETCH

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