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Understanding Recovery Is as Important as Understanding Decline: The Case of the Crested Ibis in China

Xinhai Li [1,2,*], Jiayu Fu [3], Tianqing Zhai [4], Yazu Zhang [4], Michael W. Bruford [5], Yuehua Sun [1,2] and Xiangjiang Zhan [1,2]

1 Key Laboratory of Animal Ecology and Conservation Biology, Institute of Zoology, Chinese Academy of Sciences, Beijing 100101, China
2 College of Life Sciences, University of Chinese Academy of Sciences, Beijing 100049, China
3 Beijing National Day School, 66 Yuquan Road, Haidian District, Beijing 100039, China
4 Shaanxi Hanzhong Crested Ibis National Nature Reserve, Yang County, Hanzhong 723300, China
5 Cardiff School of Biosciences, Sir Martin Evans Building, Cardiff University, Museum Avenue, Cardiff CF10 3AX, UK
* Correspondence: lixh@ioz.ac.cn; Tel.: +86-10-64807898

Abstract: The wild population of the crested ibis (*Nipponia nippon*) has recovered remarkably from seven individuals in 1981 to over 7000 in 2021. However, it is unclear how key factors, from endogenous density dependence to exogenous environmental pressure, have contributed to the species' recovery. We used species distribution models to quantify the contributions of climatic variables, human impact, land form and land use in order to understand the recovery process in the context of prevailing environmental conditions. We also calculated the nest density over the past 39 years to estimate the influence of density dependence on population dynamics. We found that the interaction between rice paddy areas and water bodies (rivers, lakes and ponds) had the highest contribution to nest site selection, whereas linear terms for either rice paddies or water bodies alone had little effect. During its recovery, sub-populations in two watersheds have been constrained by high density and have experienced logistic growth, while other sub-populations in over seven watersheds are growing exponentially. Our models indicate that exogenous environmental factors are more important than density restriction at this stage. In China's transformed landscape, the crested ibis needs both rice paddies and water bodies to fulfil its annual life cycle. Habitat protection should thus cover both habitat types to ensure the long-term survival of this still endangered species.

Keywords: carrying capacity; population dynamics; interaction effects; model selection; nest site selection; species distribution models (SDMs); watershed; wetland

Citation: Li, X.; Fu, J.; Zhai, T.; Zhang, Y.; Bruford, M.W.; Sun, Y.; Zhan, X. Understanding Recovery Is as Important as Understanding Decline: The Case of the Crested Ibis in China. *Land* **2022**, *11*, 1817. https://doi.org/10.3390/land11101817

Academic Editor: Stephen Blake

Received: 23 September 2022
Accepted: 14 October 2022
Published: 17 October 2022

1. Introduction

Recent decades have witnessed numerous species extinctions and population declines [1,2], but some endangered species have fortunately recovered for reasons that are not always clear [3]. In the United States, 23 species were identified as recovered, and 43 species were downlisted from endangered to threatened or removed entirely from the Endangered Species List between 1973 and 1999 [3,4]. Among these species, the mechanism of recovery is largely unknown, e.g., [5,6]. For example, peregrine falcon (*Falco peregrinus*) populations have been restored in the past 40 years starting from about 300 to over 7000 individuals after the ban on DDT in early 1970s, yet the mechanism of such population growth has not been sufficiently addressed [7]. Varied reasons, e.g., [8], have been proposed to account for the recovery of the bald eagle (*Haliaeetus leucocephalus*), but the underlying recovery process is still unknown. In general, a challenging question in regards to recovered/recovering species remains the same: what are the prevailing factors that have driven the population to rebound [3]?

The recovery of the crested ibis (*Nipponia nippon*) presents an ideal model to address this issue, because, unlike many other recovered species, which lack detailed information about their demography and environmental factors, the entire wild population has been closely monitored since its recovery [9]. The crested ibis used to be a common species in East Asia [10,11]. Due to the massive use of pesticide and fertilizer in rice paddies, the crested ibis' favorite foraging sites, as well as habitat loss and human disturbance, the wild populations underwent a rapid decline [10,12]. In 1963, Russia declared the birds locally extinct; in 1975, the last crested ibis disappeared from North Korea; in 1981, the last five known survivors were put in captivity in Japan, yet they never successfully reproduced [10]. Fortunately, two breeding pairs and three nestlings were rediscovered in Yang County, Shaanxi, Central China in 1981 [13]. Since then, the species has been recognized as one of the world's most critically endangered bird species [14], and numerous efforts by governments and society have been undertaken to conserve this species using *in situ* and *ex situ* conservation [15,16]. After a continuous population increase for four decades, the population size is estimated to have reached over 7000 wild individuals in 2021 [9]. The ibis has also been reintroduced into Japan [17] and South Korea [18], and to several putative historical locations in China [16]. Although the crested ibis population has been continuously monitored throughout its recovery processes, e.g., [13,19,20], until now there has been no systemic study investigating why and how the species recovered.

Two hypotheses may explain the recovery of the crested ibis. The first is that if the habitat is restored, the species will respond positively, and the population will grow exponentially until other limiting factors start to play a role. Our previous work has indicated that the habitats have improved mainly because of the banning of pesticide and fertilizer use in its core habitat [9], with the contamination of rice paddies is speculated to be an important condition associated with the population decline [12]. The second hypothesis associated with the crested ibis' recovery is density dependence, e.g., [21], in which the birds have a high growth rate at low densities and its population growth would become restricted at high densities. The crested ibis has been found to compete for limited food resources during breeding [22,23] because rice paddies serve as their main breeding foraging sites [24]. The two hypotheses explain both exogenous (environmental) and endogenous (demographic) reasons for the species' recovery, but remain untested until now.

Here, through the continuous collection of nesting data from 1981 to 2019, we systematically analyzed the contributions of environmental variables (climate, anthropogenic influence, land class and land use types) in the habitat selection of the crested ibis, and estimated their population density in different regions and at differential temporal stages, with the aim to explore whether the two hypothetical mechanisms or their interactions are responsible for the successful species recovery of this endangered species.

2. Methods

2.1. Study Area and Nest Data Collection

Having recovered from a few remnant individuals, the wild population of the crested ibis resides in Yang County and its neighboring counties in Shaanxi Province, Central China. Yang County is on the southern slope of the Qinling Mountains (Figure 1). The landscape comprises forested foothills and steep mountains to the north and gently rolling croplands in the south, mixed with rivers and ponds. The species' typical nesting habitat has been described as temperate forest mixed with rice paddies and other wetlands [13,20].

We collected annual nesting data for the recovering population in Yang County and the adjacent areas from 1981 to 2019. The crested ibis has strong nest site fidelity [24], and we therefore checked all the nest sites used, surveyed potential sites using line transects, and recorded the presence or absence of birds at those sites. We determined a survey route for each nest. Most survey routes are fixed and have been repeatedly used for many years. Occasionally, surveyors made a detour in order to find new nests. The crested ibis is a large bird, which can be easily detected in forests, shrubs and crop lands. As such, the survey time was in the daytime (7:00–19:00), unlike song bird surveys that start at dawn. Surveys for the crested ibis were repeated 3–4 times per breeding season. As a result, we recorded 3366 nest sites based on the 39-year-long survey (Figure S1).

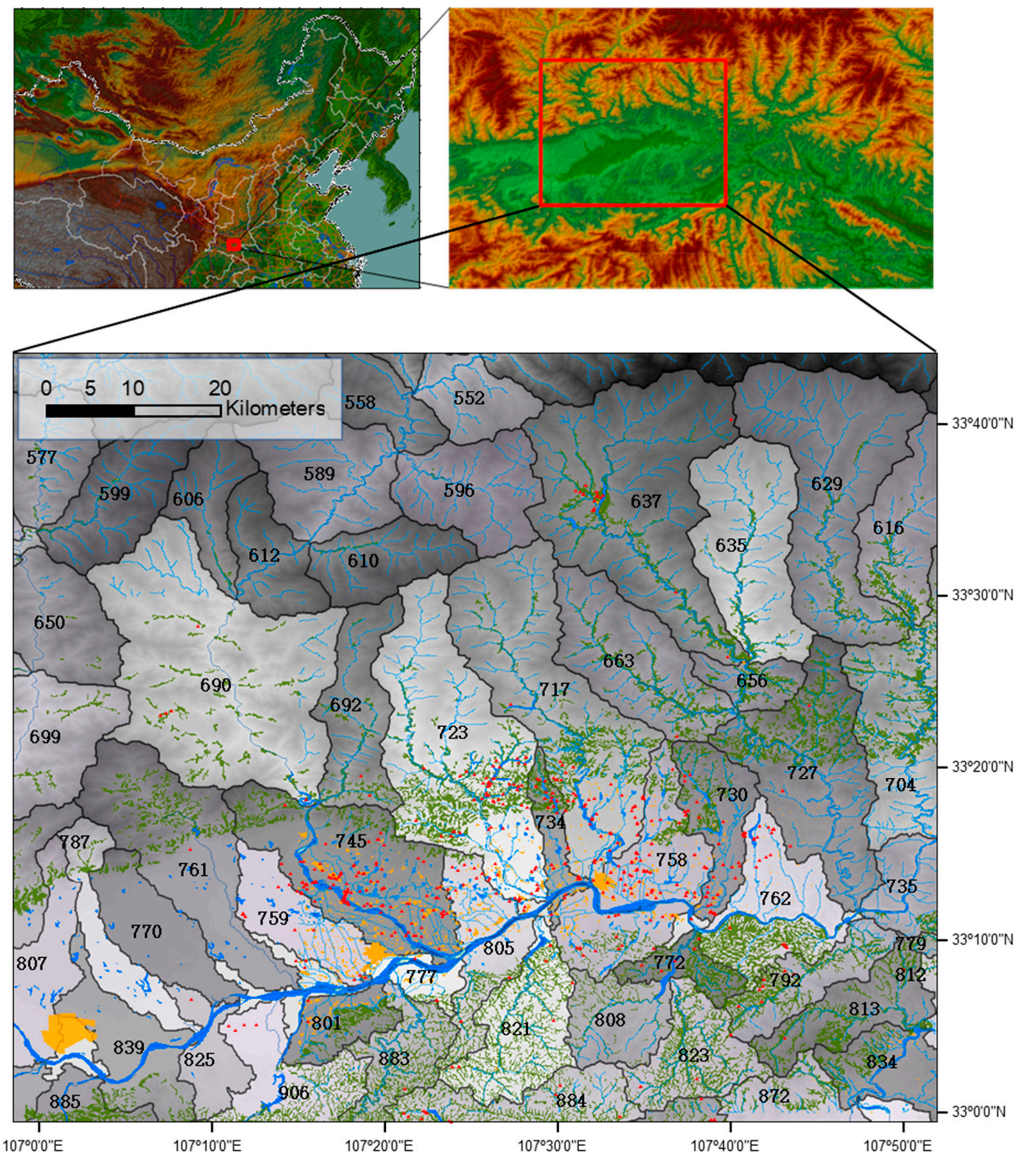

Figure 1. The spatial distribution of crested ibis nest sites in 2019 (red triangles). The upper right panel shows the elevation of the study area, ranging from 400 to 1800 m. In the bottom panel, the polygons in grey colors are watersheds; the green areas represent rice paddies; the blue areas represent water bodies (rivers, lakes, and ponds); and the brown areas are human residences.

2.2. Using Watersheds as the Spatial Scale for Habitat Analysis

The accuracy of species distributions predicted by species distribution models (SDMs) may suffer from spatially and/or temporally autocorrelated occurrence observations [25,26]. To overcome this bias, we analyzed the habitat use of the crested ibis at the scale of the watershed, evaluating the overall suitability of each potentially occupied watershed. The birds stay in the same watershed during the breeding season (due to limited dispersal of less than 10 km [12]). Watersheds were delineated using DEM (digital elevation model) data using HydroSHEDs developed by the WWF-US [27,28]. Watershed area was at 100–200 km^2 (Figure 1) in order to cover both breeding and post-breeding habitats. With this standard, 95 watersheds were defined in our study with an average area of 154 km^2 (Figure 1). We then used negative binomial regression models to explore the relationship between the number of nests in a watershed and local environmental variables. Analysis at a larger spatial scale, rather than using point occurrences, also enabled us to examine the overall habitat preference throughout the species' life cycle.

2.3. Environmental Variables

We constructed a GIS database with a layer of crested ibis occurrences using the nest site data collected above (Figure S1), and seven other layers with nine environmental variables related to climate, land use, land form and human impact: annual mean temperature, annual total precipitation, area of rice paddies, area of water bodies, mean elevation, variance in elevation, human population density, human footprint index and gross domestic product (GDP). Two elevation variables were derived from the DEM layer, and areas of rice paddies and water bodies were derived from the land use layer.

The means, standard deviations and ranges of these variables, as well as the data sources, are listed in Table 1. Elevation data were taken from the Shuttle Radar Topography Mission (SRTM) dataset at a horizontal resolution of 90 m [29]. Land use data comprised polygons identified as cropland (irrigated or non-irrigated), forest, shrub, grassland, or water bodies (i.e., rivers and ponds), derived from remote sensing images processed by the Chinese Academy of Surveying and Mapping [30]. The irrigated croplands in the study area were all rice paddies. Human population density and gross domestic product (GDP) were raster layers at a resolution of one km^2, processed by the Institute of Geographic Sciences and Natural Resources Research, Chinese Academy of Sciences [31,32]. The human footprint index was a raster layer integrating impacts of human population density, accessibility, land transformation and electrical power infrastructure at a resolution of one km^2 [33]. The annual average temperature and total precipitation were raster layers calculated from monthly mean values from 1971 to 2000 [34].

To check the multicollinearity of the environmental variables, we used variance inflation factors (VIFs) to quantify the dependence of a variable with all other variables. The vif function in R package car [35] was used to calculate VIFs. We removed variables with VIF scores over 5.

Table 1. Variable parameters and data sources used in the nest site selection analysis of crested ibis.

Variables Measured within Each Watershed	Parameters				Unit	Source
	Mean	Minimum	Maximum	SD		
Area	154.11	32.65	474.66	99.59	square km	(Rabus et al. 2003) [29]
Mean elevation	1018.32	508.43	1891.37	394.91	m	(Rabus et al. 2003) [29]
SD of elevation	243.48	28.84	601.06	121.95	m	(Rabus et al. 2003) [29]
Area of rice paddies	1.67	0.00	12.95	2.31	square km	(Chinese Academy of Surveying and Mapping 2004) [36]
Area of water bodies	0.12	0.00	1.03	0.19	square km	(Chinese Academy of Surveying and Mapping 2004) [36]
Population density in 2000	190.36	3.93	1387.31	234.86	person per square km	(Data Center for Resources and Environmental Sciences 2006b) [32]
GDP in 2000	45.34	0.69	453.23	78.75	1000 RMB per capita	(Data Center for Resources and Environmental Sciences 2006a) [31]
Human footprint index	25.04	14.62	47.62	6.67	/	(Sanderson et al. 2002) [33]
Annual mean temperature from 1971 to 2000	12.37	7.61	14.78	1.98	degree Celsius	(China Meteorological Administration 2012) [34]
Annual total precipitation from 1971 to 2000	878.44	803.36	1049.88	54.57	mm	(China Meteorological Administration 2012) [34]

2.4. Species Distribution Modelling

Since the number of nests within the 95 watersheds are count data, and the variances of the data are about 10 times higher than the mean values, we applied negative binomial regressions to explain the annual number of nest sites within the watersheds using nine explanatory variables (Table 1). At watershed i, the number of nests inside the watershed is N_i, estimated by:

$$log(N_i) = b_0 + \Sigma(b_m \times var(i, m)) \quad (1)$$

where b_0 is the intercept, b_m is the mth coefficient, and $var(i, m)$ is the mth explanatory variable or term (e.g., quadratic term or interaction term) of watershed i.

Equation (1) represents a full model including all the linear terms, quadratic terms, and two-way interaction terms between the explanatory variables. We ran a negative binomial regression model to fit data for each year from 1993 to 2019, because the sample sizes (number of nests) were too low before 1993. We used a backward stepwise model selection procedure based on AIC values. All remaining variables and terms are listed in Table S1.

Since the performance of the negative binomial regressions was not stable across years from 1993 to 2019, we also used multiple regression models to quantify the association between the number of nests in watersheds and the environmental variables of watersheds. The models are:

$$N_i = b_0 + \Sigma(b_m \times var(i, m)) \quad (2)$$

In the multiple regressions, we selected the type III sum of square to quantify the contribution of each variable/term by using the Anova() function in the package car [35]. Backward stepwise model selection procedure was also carried out, and the results were listed in Table S2.

Negative binomial regression models and multiple regression models, although they take into account all the quadratic and two-way interaction terms as types of linear models, poorly fit the dependent variable (number of nests) if the nonlinearity, interaction and multicollinearity of the explanatory variables are strong. As such, we applied a random forest approach [37] to predict the number of nests in all watersheds and evaluated the contributions of the explanatory variables. We included all nine explanatory variables in the model, ranked their importance, and plotted the partial effects of these variables. The random forest can also facilitate the model selection of the negative binomial regressions, as we can select the most important variables and relevant terms based on the random forest importance indices and partial plots. Specifically, the quadratic term of a variable was kept in the model when the partial plot showed a dome-shaped curve.

2.5. Nest Density and Carrying Capacity Estimation

To access the nest density in each year, we counted the number of nests within the rectangle enclosing all the nests in the year and calculated the nest density as: number of nests/area of the rectangle. Since 2000, a few nests have been far away from others. As such, we used the 10% and 90% quantile ranges of latitude and longitude to define the rectangle, meaning we estimated nest density in the central part of the nesting areas. We also calculated distances between every two nests in every year, as an index of population density.

To estimate the carrying capacity for the crested ibis in its current distribution range, we applied a random forest algorithm to calculate the presence of nests using all nest sites in 2019 and 900 evenly distributed pseudo-absence points. We used the R package abundanceR [38], which provided 39 variables covering all terrestrial areas on the earth, and provided functions to crop the environmental data layers (function: cropLayers()), generate pseudo-absent points, extract values of environmental variables (function: getEnvData()), develop SDMs and make the prediction at a one km^2 resolution (function: popSize()). The predicted presence using an SDM is usually not accurate, unless the target species reaches carrying capacity or follows an ideal free distribution [39]. As such, we used the ratio of predicted and observed number of nests in watersheds where the ibis population has reached carrying capacity to adjust the estimated nest numbers. We also predicted the number of nests within watersheds directly using the environmental variables of watersheds based on the random forest algorithm.

3. Results

From 1981 to 2019, the crested ibis population gradually increased from only two breeding pairs in two watersheds to 511 breeding pairs occupying 35 watersheds in the Hanzhong Basin, including 503 pairs in 32 watersheds in the central part of the Hanzhong Basin (Figure 1 and Figure S1). Initially, the population fluctuated at a very low level (two to four pairs) for 13 years after its rediscovery. From 1994, the population started to increase rapidly. Generally, its demographic recovery can be fitted using an exponential function: number of nests = exp (1.445 × (−1977 + Year)) (Figure 2, upper panel). The R^2 value of the regression reached 98%. However, the sub-population growth varied among different watersheds: sub-populations reached carrying capacity in watersheds 723 and 717, featuring large subpopulation sizes (number of nests were 43 and 31, respectively) and population stability by 2006 and 2015, respectively, whereas others (i.e., watersheds 745, 758, 732, 762, 637, 734 and 805) demonstrated continual exponential growth (Figure 2).

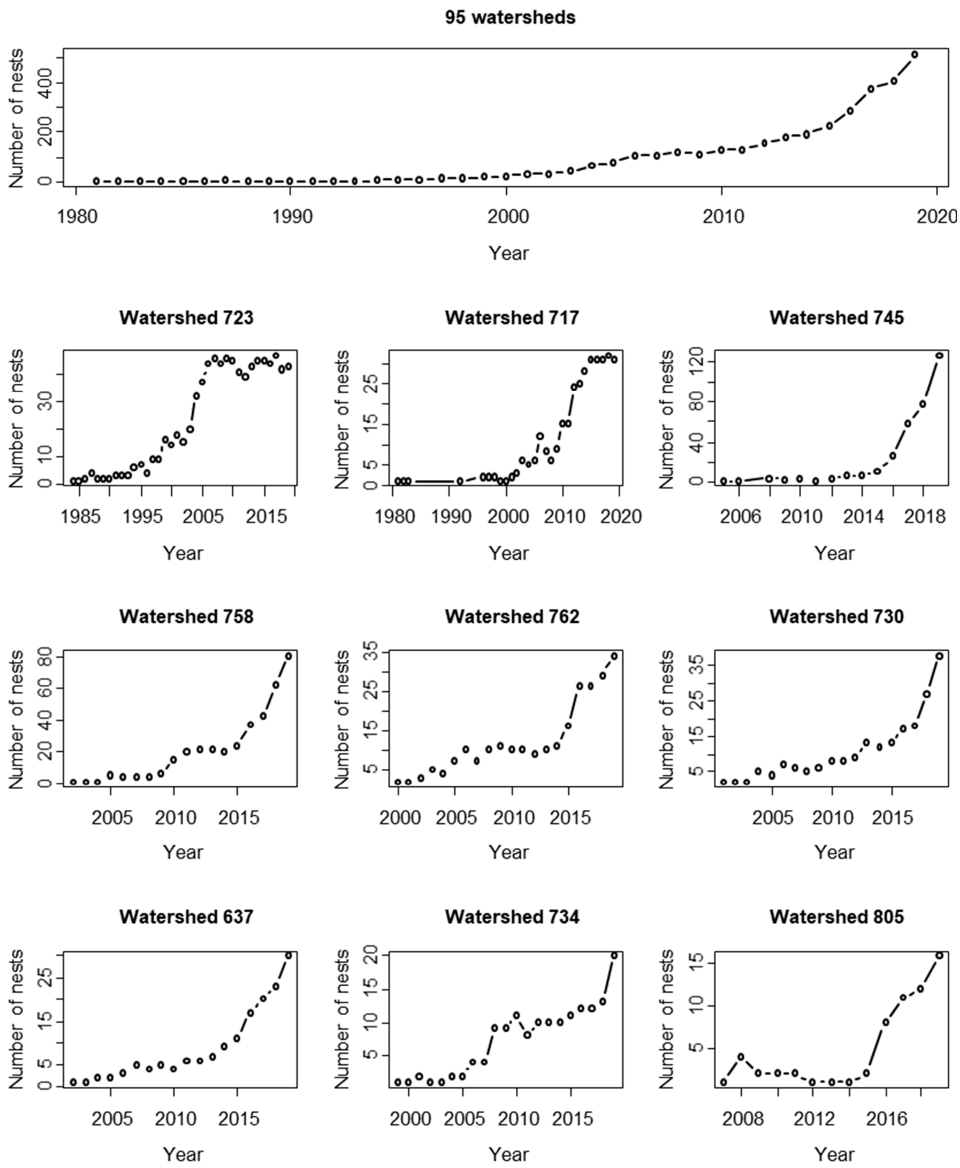

Figure 2. Number of nests of the crested ibis from 1981 to 2019 in its whole habitat (upper panel) and in the nine most occupied watersheds (lower panel).

We checked the independence of the environmental variables and found that six variables, mean elevation, standard deviation of the elevation, annual total precipitation, human population density, areas of rice paddies and areas of waterbodies, have VIF scores less than five, and we used these variables to build the negative binomial models. Temperature was removed, as its correlation coefficient with elevation was −0.99. GDP and human footprint index were also removed because their correlation coefficients with human population density were 0.93 and 0.83, respectively.

The results of 27 negative binomial regressions for the years from 1993 to 2019 showed that the most important term is the interaction term of areas of rice paddies and areas of waterbodies. The elevation–population interaction was also important in some years. Other important variables are areas of water bodies, areas of rice paddies, square term of elevation, standard deviation of elevation (ElevSD), etc. (Tables 2 and S1). The results of the multiple regressions are similar (Tables 2 and S2), and they provided a consistent contribution of variables across the 27 years (Figure 3), compared with those from the negative binomial regressions (Figure S2).

Table 2. The most important variables and terms in negative binomial regressions and multiple regression that fit number of nests in watersheds by environmental variables.

Negative Binomial Regressions			Multiple Regression		
Variable/Term	**Proportion of Deviance (Mean Value) ***	**Significance in 27 Years ****	**Variable/Term**	**R Square (Mean Value)**	**Significance in 27 Years ****
Elevation	0.064	19	Elevation	0.033	26
Elevation:Population	0.538	5	Elevation:Rice_paddy	0.058	27
ElevSD	0.122	24	ElevSD^2	0.026	26
Elevation^2	0.144	18	Population	0.021	9
Population^2	0.050	19	Rice_paddy	0.033	24
Rice_paddy	0.061	24	Rice_paddy:ElevSD	0.044	25
Rice_paddy:Wter_body	0.340	10	Rice_paddy:Waer_body	0.198	27
Water_body	0.169	24	Water_body	0.038	21
			Water_body:ElevSD	0.042	21

* The proportion of deviance decreased when the variable/term was added to the model. Mean values are the values for models for years from 1993 to 2019. ** The number of times the variable/term was significant among the 27 models for years from 1993 to 2019.

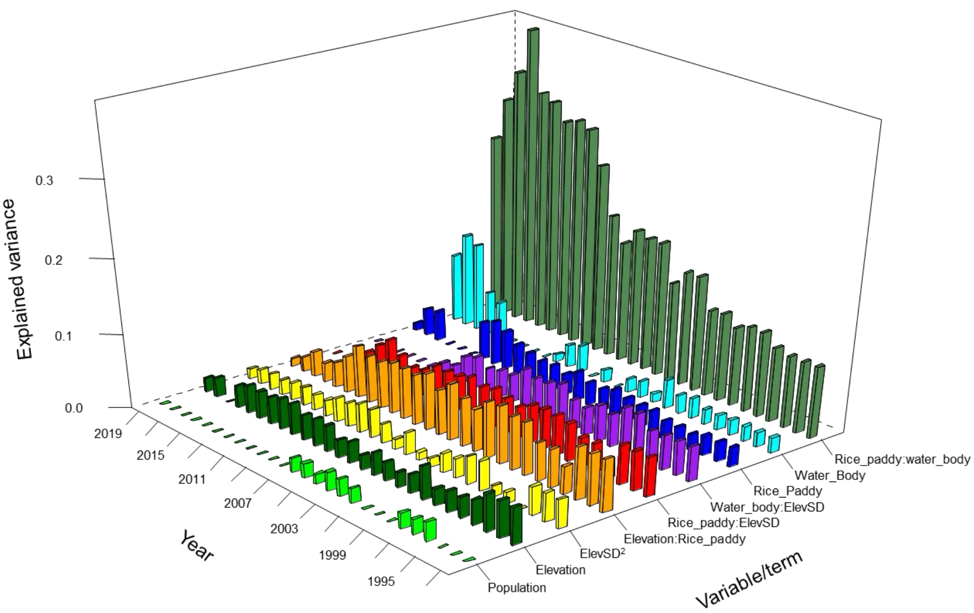

Figure 3. Contribution (proportion of explained variance) of variables/terms in the multiple regressions fitting the number of nests in the watersheds from 1993 to 2019.

Our random forest models included all the correlated variables because random forest is robust to multicollinearity. The interaction term of areas of rice paddies and water bodies was especially important, thus we added this term (areas of rice paddies × areas of water bodies) to the random forest model as a variable and named it "Wetland". The results showed that in 2019, the most important explanatory variables for nest selection were the interaction term of areas of rice paddies and water bodies (the Wetland in the model), areas of water bodies, areas of the watersheds and standard deviation of elevation (Figure S3). Based on the partial plots (Figure S4) of the explanatory variables, we can see that precipitation had a bow-shaped effect, so that the quadratic term of precipitation might be included in the linear models.

The growth of the crested ibis population was found to be density-dependent. In watershed 723, the number of nests has been stable since 2005, and in watershed 717, the number of nests has reached carrying capacity since 2015. The population density in watersheds 723 and 717 was 0.139 and 0.102 nests/km^2, respectively. In contrast, the number of nests in watersheds 745, 758, 730, 762, 637, 734 and 805 increased dramatically after 2015. Watershed 745 became the most occupied watershed in 2017 (Figure 2). The bird density increased asynchronously in different watersheds.

During the recovery of the crested ibis, the population density increased steadily after 2000 (Figure S5). One striking feature is that many crested ibises no longer defend their breeding territories, and nest together with others. From 1994 to 2005, the minimum distance between nests was 100 m; since 2005, the minimum distance has been 10 m, and since 2016, more pairs have nested in the same trees (Table 3).

Table 3. The number of cases that the distance between every two nests is less than a series of thresholds indicating the number of neighboring nests in each year.

Year	No. of Nests	No. of Distance <10,000 m	No. of Distance <1000 m	No. of Distance <100 m	No. of Distance <10 m	No. of Distance <1 m
1993	3	2	0	0	0	0
1994	6	14	1	1	0	0
1995	7	21	2	1	0	0
1996	6	10	0	0	0	0
1997	11	44	2	0	0	0
1998	11	54	2	0	0	0
1999	18	147	14	1	0	0
2000	20	117	13	3	0	0
2001	30	220	19	3	0	0
2002	31	153	8	2	0	0
2003	42	312	22	3	0	0
2004	62	721	60	6	0	0
2005	78	956	77	7	1	0
2006	105	1655	114	2	1	0
2007	106	1510	86	13	9	0
2008	118	1736	80	5	0	0
2009	112	1765	78	3	0	0
2010	128	2373	79	0	0	0
2011	129	2178	61	1	1	0
2012	153	2796	61	1	1	0
2013	177	3588	78	3	2	0
2014	189	3902	100	5	2	0
2015	220	4759	137	11	4	0
2016	286	6992	191	35	14	1
2017	368	9695	271	53	26	1
2018	405	14,115	543	75	40	2
2019	511	26,194	1019	162	58	2

We used two methods to predict the number of nests based on the environmental variables (Table 1) using the random forest algorithm: the occurrence-based method (Figure 4, left panel) and the watershed-based method (Figure 4, right panel). The former method overestimated the number of nests, and the latter method underestimated the number of nests (Table 4). We adjusted the predictions using the number of nests in watersheds 717 and 723, where the bird populations reached their carrying capacity and were stable for years (Figure 2). Compared with the number of nests in watersheds in 2019, the watershed-based method provided more accurate predictions (Table 4), because it explained 94.6% of the variance in the number of nests in all watersheds, whereas the occurrence-based method explained 77.2%.

Based on the watershed-based method, we found that watersheds 777, 906 and 801 had a large capacity to support more birds. Watersheds 770, 807 and 635, although not occupied, were suitable for the crested ibis and can support 5–7 pairs. The carrying capacity of the 95 watersheds is 602 pairs (Table 4).

Table 4. The observed number of nests in each watershed, predicted number of nests and adjusted number of nests using occurrence-based method and watershed-based method, respectively.

Watershed	No. Nests in 2019	Predicted_Point *	Predicted_Polygon **	Adjusted_Point *	Adjusted_Polygon **
745	126	196.5	76.0	53.0	91.8
758	81	188.1	67.0	50.7	81.0
723	43	154.4	37.6	41.6	45.5
730	38	70.1	20.9	18.9	25.2
762	34	97.9	27.9	26.4	33.7
717	31	119.0	24.2	32.1	29.2
637	30	37.7	27.8	10.2	33.6
734	20	44.1	14.7	11.9	17.8
805	16	83.9	11.1	22.6	13.5
884	15	95.9	17.7	25.8	21.4
759	10	69.2	15.3	18.7	18.4
792	8	41.7	6.0	11.2	7.2
821	6	68.9	7.1	18.6	8.6
690	5	51.9	3.7	14.0	4.5
777	5	22.1	14.3	6.0	17.3
772	4	35.3	4.7	9.5	5.7
846	4	26.7	5.5	7.2	6.7
906	4	30.6	7.7	8.3	9.3
727	3	51.3	2.9	13.8	3.5
801	3	20.7	7.6	5.6	9.2
823	3	49.2	4.2	13.3	5.1
692	2	12.0	1.1	3.3	1.3
779	2	18.6	3.4	5.0	4.1
813	2	19.6	3.5	5.3	4.2
629	1	7.7	1.2	2.1	1.4
663	1	16.6	1.1	4.5	1.4
748	1	6.9	1.4	1.9	1.7
761	1	47.5	2.3	12.8	2.8
763	1	11.6	4.0	3.1	4.8
808	1	31.7	2.0	8.5	2.4
825	1	14.7	4.2	4.0	5.0
883	1	44.2	2.4	11.9	2.9
770	0	17.7	5.8	4.8	7.0
807	0	7.3	5.4	2.0	6.5
635	0	7.8	4.6	2.1	5.6
774	0	0.1	3.9	0.0	4.8
839	0	9.2	3.7	2.5	4.5
876	0	11.8	3.4	3.2	4.1
Total	503	2144	499	578	602

* Predicted and adjusted number of nests in each watershed using the occurrence-based method.** Predicted and adjusted number of nests in each watershed using the watershed-based method.

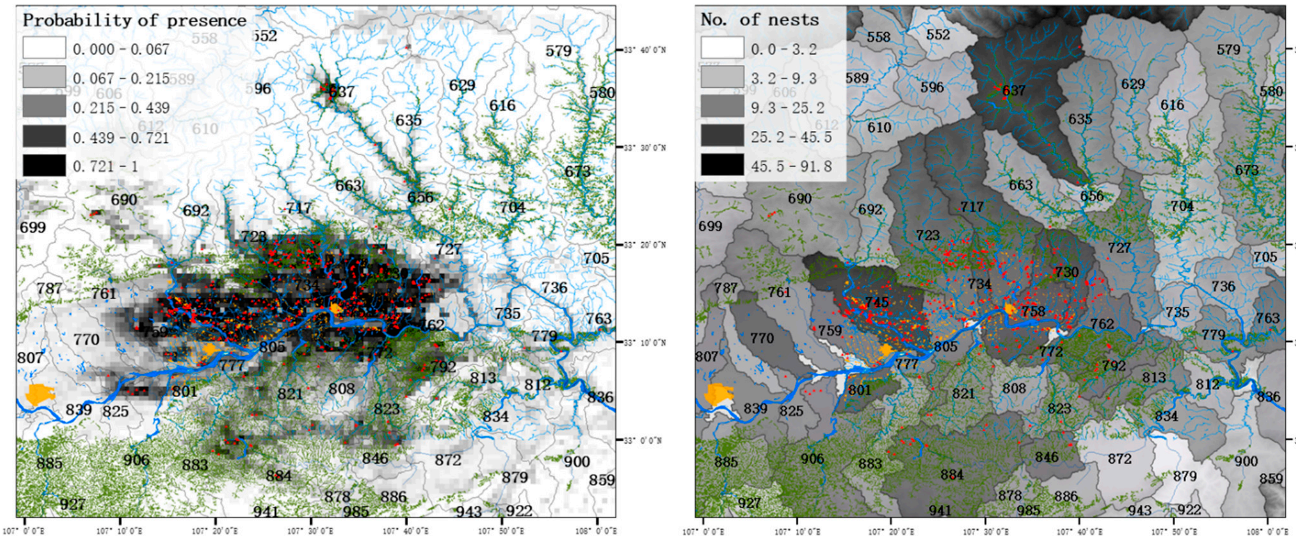

Figure 4. Predicted probability of presence of nests in every 1 km^2 quadrat (left panel) and predicted number of nests in every watershed based on the nest data in 2019 using the random forest algorithm (right panel). The probability of presence was summed in every watershed to represent number of nests. The red triangles are nest sites. The polygons in grey colors are watersheds; the green areas represent rice paddies; the blue areas represent water bodies (rivers, lakes, and ponds); and the brown areas are human residences.

4. Discussion

The crested ibis has recovered from seven individuals (two pairs and three nestlings) [13] to over 7000 from 1981 to 2021 (including several captive populations), making it a conservation success story of global significance [9]. Previous studies have suggested that the most important reasons for its recovery are habitat restoration (e.g., pesticide ban) and poaching control [11,16,19,40]. In this study, we demonstrated that the habitat combination of rice paddies and water bodies played the most important role in habitat selection, while previous studies only implicate the importance of wetlands without distinguishing wetland types, e.g., [22,41–43]. We highlight that the crested ibis needs both rice paddies and water bodies in watersheds. In general, habitat quality (in term of the areas of rice paddies and water bodies) was the most important factor for the ibis' recovery, rather than human disturbance and climate conditions [44]. Thus, the hypothesis that environmental factors dominated the recovery of this species is supported, since the population has grown as a function of habitat restoration and availability [9].

The SDM analysis allowed us to estimate the carrying capacity to be 602 nests (Table 4) in the 95 watersheds, meaning that the population is expected to reach its carrying capacity in a few years, if the ibis population keeps growing at its current rate (Figure 2), even though density dependence may slow this growth as the carrying capacity is approached and available nesting sites in other watersheds become limiting. The dependence on wetlands constrains the bird's distribution within the Hanzhong Basin, which has a high density of wetlands (Figure 1, upper right panel). The area adjacent to the Hanzhong Basin is likely to be too dry for the crested ibis, so that the carrying capacity of 602 nests is unlikely to increase substantially if the population was to expand its range.

The dramatic increase in population density from 1993 to 2019 implies that there is no density-dependent limitation on population recovery. However, the logistic population growth in two watersheds (the core habitat) showed that high densities can constrain population growth in some regions. In watersheds 717 and 723, population growth seems to have stopped a few years ago (Figure 2) since the available foraging sites, the rice paddies along the river, are now all occupied.

During the recovery process, the crested ibis has shifted to lower altitudes with higher human densities, from about 1200 m in 1980s to 600–800 m in 2000s. In recent years, especially since 2015, over 50 new nests have been built in the lowest area of the region, where the human population density is very high. For example, the human density in watershed 745 is 715 person/km^2.

The area of rice paddies and water bodies are the most important factors for nest site selection by the crested ibis, implying that food supply is the limiting factor for birds during the breeding season. The bird therefore requires both wetland types, but in different seasons. During the breeding season, rice paddies are the major foraging sites. The rice paddies in the area (Figure 1) are mostly permanent (i.e., rice is harvested once in a year, and then the paddies are left fallow), as the local weather is not warm enough for two harvests in a year, compared to elsewhere in Southern China. The rice paddies usually have rich food resources, such as fish and invertebrates. In June, the breeding season ends and the rice plants are too high and dense to be accessed by the crested ibis. At this time, adults bring their fledglings to low-elevation areas, where they can forage around the water bodies (i.e., rivers, ponds and lakes). Thus, watersheds featuring both rice paddies and water bodies are the preferred habitat, as they can support the full life cycle of the bird.

In the study area, all streams are natural without dams or levees. However, there are lots of man-made ponds and reservoirs, contributing about 20% of the water body areas. Moreover, all the rice paddies are non-natural. As such, the aquatic habitat of the crested ibis is half-natural. We think the crested ibis is a "smart" bird that rapidly adapted to human-altered habitats, and became a human-commensal bird species.

Selecting an appropriate sampling scale is important in habitat modeling [45]. We selected the watershed as our unit of analysis. The results contrast those from previous studies that were based on the occurrence data and raster layers of environmental variables, e.g., [12,24], which only addressed its habitat preference in one season (i.e., the breeding season). We suggest using region-based SDMs to study species–environment relationships, which would provide more general information about the overall suitability of a region. However, one weakness of region-based SDMs is that they cannot address spatial heterogeneity at a fine scale (i.e., quadrat scale with a 1 km^2 resolution) within a watershed. Further studies could focus on fine-scale analyses within watersheds in which the carrying capacity has been reached and make comparisons to those in which it has not been achieved.

Among the iconic recovered birds of the world, few species have been as closely monitored with detailed demographic data as the crested ibis, with notable exceptions, including the Mauritius kestrel [46] and California condor [47], yet the use of spatially explicit population information for recovering species is rare [3]. Using accurate nest location data over the past 39 years, we were able to analyze the dynamics of habitat preference (Figure 3) and population density (Figure S1), showing the changes in the contribution of key factors (rice paddies and water bodies) for recovery (Table S1).

Finally, we have demonstrated the asynchronous population growth of the crested ibis in different watersheds and predict that growth will slow or stop in a few years, since our model suggests that there is still space in the lower elevation areas of the region, but that this space will be exhausted soon. We concluded that areas of rice paddies and water bodies are the most important factors in the crested ibis' recovery and suggest that the bird can live harmoniously with local farmers as long as poaching is controlled and pesticide usage is restricted in this region.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/land11101817/s1. Figure S1. The locations of nests built by the crested ibis from 1981 to 2019. Figure S2. Contribution (proportion of deviance decreased) of variables/terms in the negative binomial regressions fitting the number of nests in the watersheds from 1993 to 2019. Figure S3. Variable importance in the random forest model explaining the variance of the number of nests in 95 watersheds in 2019. Variable wetland is the interaction term for areas of rice paddies and areas of water bodies. Figure S4. Partial effects of each variable on the number of nests in watersheds in 2019 based on the random forest algorithm. The variables were ranked in descending importance order in the plot. Figure S5. Population density (number of nests per km^2) of the crested ibis in Hanzhong, China from 1981 to 2019. Table S1. The remaining variables and terms after stepwise model selection of the negative binomial regressions fitting the number of crested ibis nests within watersheds from 1993 to 2019 based on the environmental variables of the watersheds. Table S2. The remaining variables and terms after stepwise model selection of the multiple regressions fitting the number of crested ibis nests within watersheds from 1993 to 2019 based on the environmental variables of the watersheds.

Author Contributions: Conceptualization, X.L., X.Z. and Y.S.; methodology, X.L.; validation, T.Z. and Y.Z.; formal analysis, X.L.; investigation, X.L., J.F. and T.Z.; data, X.L. and T.Z.; writing—original draft preparation, X.L.; writing—review and editing, X.L., J.F., M.W.B. and X.Z.; visualization, X.L.; supervision, Y.S.; project administration, X.L.; funding acquisition, X.L. All authors have read and agreed to the published version of the manuscript.

Funding: This work was supported by the National Natural Science Foundation of China (No. 31970432 and 32171528), the Strategic Priority Program of Chinese Academy of Sciences (XDB31000000), the Third Xinjiang Scientific Expedition Project (Grant No. 2021XJKK1302), and the Second Tibetan Plateau Scientific Expedition and Research Program (STEP, Grant No. 2019QZKK0501). The study is also supported by the Alliance of International Science Organizations (ANSO) (Project ID: ANSO-CR-KP-2020-08) for ecosystem safety assessment and policy making at the China–Mongolia–Russia corridor of the One Belt One Road zone.

Data Availability Statement: The number of nests in 95 watersheds from 1981 to 2019 and associated environmental variables are provided as a supplementary EXCEL file (watersheds-number of nests and environmental variables.xlsx). The nest locations are sensitive data regarding conservation, and they are available upon request.

Acknowledgments: We thank the staff of Hanzhong Crested Ibis National Nature Reserve for their help during the field surveys. We are grateful to Liming Ma for carrying out the field surveys.

Conflicts of Interest: The authors declare no conflict of interest.

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