

## Roosting-site Selection by Overwintering Black-necked Cranes in the Caohai Wetland, Guizhou Province, China: Implications for Conservation Management

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The stable and high-quality roosting-sites are crucial for the survival of migratory wading birds in winter. The black-necked crane (*Grus nigricollis*) is the only crane species that lives on the Tibetan plateau for its entire life. Every year, black-necked cranes routinely migrate to the wetlands on the southern lower plateau and roost at wetland sites. Currently, many roosting sites are under threat from wetland degradation resulting from human disturbance, changes in water depths and the landscape environment. To understand how the black-necked crane selects roosting sites given these influencing factors, we conducted a study in the Caohai wetland in China by comparing and modeling the selection of roosting habitat. Results: (1) The vegetation factors mainly included the vegetation height of the swamp patch where the roosting site was located (VHP) and the vegetation height in the roosting site (VHR), and the geographic factors mainly included the height of the nearest hill (HNH) and the visible range (VR). These four factors were first considered by the black-necked cranes when choosing roosting sites on the lakeshore. The roosting-site selection model of black-necked cranes was fitted as

$$P = \frac{e^{\text{Logit}(p)}}{1 + e^{\text{Logit}(p)}} \text{Logit}(p) = 1.243 + 8.397(\text{VHP}) - 7.999(\text{VHR}) - 4.105(\text{HNH}) + 1.584(\text{VR}).$$

(2) In the Caohai wetland, black-necked cranes preferred roosting sites away from human disturbances, such as villages/settlements and roads, and where the distance to main roads was > 1300 m, the distance to villages/residential areas was > 650 m, the distance to rural/service roads was > 500 m, the relatively open area with surrounding hills had a relative height < 15 m, the visible range area was > 550000 m<sup>2</sup>, and the shallow swamp area had a water depth of < 5 cm with a vegetation height < 15 cm. Outside the area of the roosting site, the surrounding vegetation height was 35 cm–60 cm. We believe that energy savings and heat loss were not the main influencing factors, but human disturbance influenced cranes roosts site selection. We first gathered data about black-necked crane selection of roosting sites in a highly complex wetland system. Based on our findings, we strongly recommend appropriately managing the habitat patches in the Caohai wetland, which will have implications for the conservation management of overwintering black-necked cranes in wetlands.

**Key words:** Caohai, China, *Grus nigricollis*, Human disturbance, Overwintering wetlands, Roosting.

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## BACKGROUND

Habitat selection relates to the environmental requirements needed by animals for survival (Falconi et al. 2015). As an important part of a habitat, a roosting site (sites for sleeping) is critical for an animal's life cycle so many roosting species can have strong selectivity toward roosting sites (He et al. 2011). Generally, the influencing factors of roost site selection by animals include the geographical environment (Chandler et al. 1995), a safe environment to prevent mortalities due to predation, a stable temperature (Elmore et al. 2004; Sprague et al. 2008), and minimal human disturbance (Wang et al. 2019). Still, the main factors always depend on the specific species and the location where roosting occurs. Many of the 15 extant species of cranes undertake roosting, but there is surprisingly little information on the roosting habits of species found in Asia. Except for the gray-crowned crane (*Balearica regulorum*) and black-crowned crane (*Balearica pavonina*) that both roost on trees, the other roosting crane species usually roost in relatively large but shallow

wetlands that is safe with minimal human disturbance (Shenk et al. 1992; Wang et al. 2019), marshes or saline-alkaline marshes, mires and shoals (Hoyo et al. 1996), and broad rivers with short vegetation (Pearse et al. 2017). Factors such as environmental and human disturbance may play a vital role in selection of crane roosting sites (Li et al. 2013; Wang et al. 2019). The black-necked cranes (*Grus nigricollis*) are among the least studied crane species, and there is sparse information regarding factors that are used to select roosting sites in winter (Li et al. 2014). General observations suggest that overwintering black-necked cranes diurnally choose to roost in valleys, shoals near the water (Li et al. 2005), shallow areas of lakes, reservoirs, or ponds (Liu et al. 2008; He et al. 2011), and islands in rivers (Lei et al. 2012). However, few studies have reported how the black-necked crane chooses roosting sites on severe winter nights. The main factors affecting this behavior, especially in wetlands with intensive human disturbance and complex environments, are unknown. Understanding this critical requirement for this species is important to develop management plans that are suitable for specific important roosting sites.

The black-necked crane, also called the Tibetan crane, breeds on the Qinghai-Tibetan Plateau, China. Six wintering areas have been identified at low altitudes of Qinghai-Tibet and Yunnan-Guizhou Plateaus (Li FS 2014). Among the wintering areas, the Caohai wetland in Guizhou Province is one of the largest wintering sites for the global population, which was estimated at 10,000-10,200, and approximately 1500-2000 cranes overwinter at the Caohai wetland (Li et al. 2003; Li et al. 2005; BirdLife International 2017; Sun et al. 2018). At Caohai, black-necked cranes usually flies out from the roosting sites to the surrounding agricultural areas to forage every morning and then fly back to roosting sites by evening (Zhao et al. 2008; Wu et al. 2020). Black-necked cranes have used the same roosting sites at lakeshore areas for years (Végvári et al. 2015). At Caohai, black-necked cranes have roosted at seven roosting sites for more than five years at each site (Sun et al. 2018). And they flock together on severe winter nights scattered among these seven roosting sites with flocks of 30 to > 300 individuals (Sun et al. 2018; see Fig. S1–4). It is not clear why the cranes appear to selectively use seven locations for roosting. In this study, we ascertain which habitat and human-related features appear to influence the selection of these sites for crane roosting.

The Caohai wetland adjoins Weining County in Guizhou Province, China. Like many other wintering wetlands, this wetland has been suffering from intense human disturbance, urban expansion, and degradation of wetland ecosystems (Ran et al. 2017). This issue is especially urgent as the government is planning to raise the water level from 2171.7 to 2173 m or expand the water area of the Caohai wetland for various purposes, potentially affecting the roosting sites of overwintering black-necked cranes (Ran et al. 2017). We determine the selectivity of roosting sites by black-necked cranes and the main influencing factors. These findings would be helpful to predict

how changes in this wetland will impact crane overwintering survival.

## MATERIALS AND METHODS

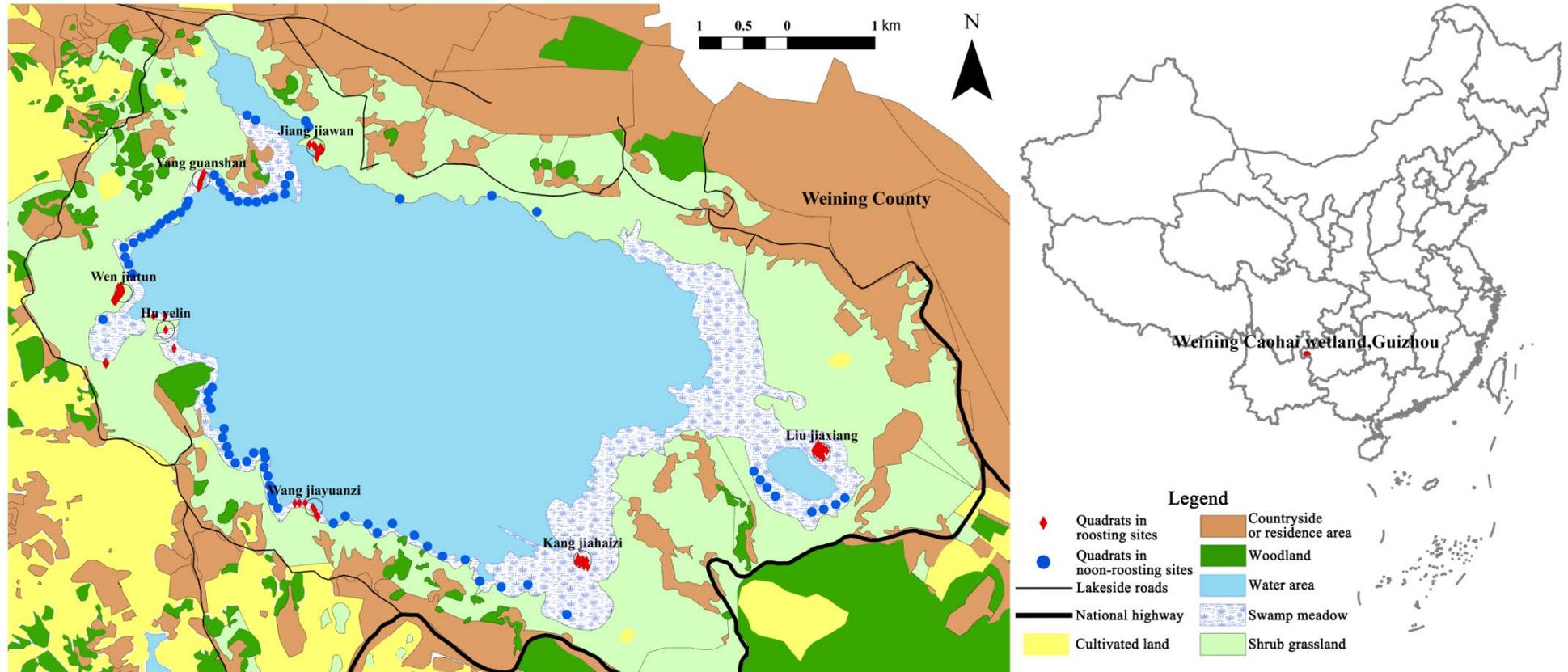
### Study Area

The Caohai wetland (China Caohai National Nature Reserve, 26°47'–26°52'N, 104°10'–104°20'E) is located in the central part of the Wumeng Mountains on the Yunnan-Guizhou Plateau in Southwest China. The total area of the Caohai Reserve is 120 km<sup>2</sup> with 25 km<sup>2</sup> encompassing water with an average water depth of 1.35 m, and the normal water level is 2171.7 m. It is the largest natural freshwater lake in Guizhou and is also a typical representative of a wetland ecosystem on the plateau in Southwest China because of its complex mix of natural habitats and human-dominated land uses (Zhang et al. 2007; Lei et al. 2017). Topographically, the Caohai wetland is plain with highlands and hills around it. Lakeshores are mainly marshes, meadows, and abandoned vegetable fields, and around the lake, there are farming lands, and several villages with more than 100 thousand inhabitants (Xu et al. 2008; Ran et al. 2017). Caohai is abundant with aquatic plants in the lake and lakeshore, such as *Myriophyllum verticillatum*, *Juncellus serotinus*, *Scirpus validus*, and *Juncus effusus*. As the primary overwintering habitat for migrating birds on the Yunnan-Guizhou Plateau, every winter, more than 70,000 waterbirds migrate to the Caohai wetland (Zhang et al. 2014). It has therefore been listed as an Asian Important Bird Area (Code: CN274) by BirdLife International (Chan 2009).

### Determining roosting sites

Although we have determined seven roosting sites of black-necked cranes by long-term routine monitoring, to obtain more specific location points we conducted additional observations from 2016 to 2019 (the end of November of the year to mid-March the following year, namely, the whole overwintering period of cranes) to locate additional sites if any. We identified a roosting site as any location that had a flock of > five black-necked cranes for at least ten days. Sites were deemed different if they were  $\geq 300$  m apart. We used a monocular telescope (SWAROVSKI-STS65HD) to observe when cranes returned from foraging sites to the lakeshore, forming flocks in the late afternoon every day. Then, cross positioning with a compass and two observation positions were conducted to determine the exact coordinates of the roosting locations on the Personal Digital Assistant maps (Liu et al. 2010). The sizes of roosting sites varied with crane flock size. The range

and area of the single swamp patch where the roosting site was mapped using ArcGIS (version 10.3.0) software. Despite additional effort to locate new roost sites, we were unable to find any beyond the seven sites that had already been documented (Sun et al. 2018). These seven sites were used for our study (Fig. 1).



**Fig. 1.** Roosting sites of black-necked cranes in the Caohai wetland, China, and the study quadrats sampled in this study.

## Investigation of influencing factors

As shown in table 1, initially, to obtain as much habitat information as possible, 14 habitat measurements that could potentially influence crane selection were measured. We categorized these 14 factors into four categories. Category I was water environment and included only water depth (WD), as we observed and previously reported (Kong et al. 2008). Black-necked cranes typically waded in water overnight, so the depth of water was considered first. Category II was human disturbance, which we measured from a distance between the surveyed quadrats and the roads, paths, villages, and farmlands, where the primary human activities occurred. Category III related to the vegetation at sites, including the vegetation height of the swamp patch where the roosting site was located (VHP), vegetation height in the roosting site area (VHR), and vegetation cover (VC). The height and coverage of vegetation on the ground often affect cranes take-off and landing because the black-necked crane has a large body and wingspan and requires preparation for take-off or landing. Category IV was a measure of the overall landscape and included the nearest distance to surrounding hills (NDH), the height of nearest hill (HNH), visible angle (VA), visible range (VR), and area of the swamp patch (ASP). We knew that these cranes always choose a place to stay overnight with no breeze to avoid heat loss in the winter (Carr 2013), but it is not practical to measure the wind and heat conditions in a vast swamp patch at certain points at night. Therefore, we determined that the surrounding hills and an open swamp patch could reflect the wind and heat conditions. In addition, crane vision is connected to alert responses toward human disturbance. We did not choose to measure food because black-necked cranes are omnivorous and because roost sites are used for sleeping and not for foraging (Sun et al. 2018).

**Table 1.** Influencing factors measured for roosting-site selection by black-necked cranes and their descriptions for the Caohai wetland, Guizhou Province, China

Category	Factors	Abbr.	Descriptions for field survey of quadrats
Water environment	Water Depth (cm)	WD	To measure the water depth from the east, south, west, north, and middle in a quadrat, and get the average value.
Interference factor	Distance to the main road (m)	DMR	The shortest straight-line distance between the center point of a quadrat and the roads where cars and trucks are allowed, measured by GIS.
	Distance to the tractor road (m)	DTR	The shortest straight-line distance between the central point of a quadrat and the tractor road, which is commonly only used by tractors among farmland area, measured by the GIS.
	Distance to the path (m)	DP	The shortest straight-line distance between the center point of a quadrat and the nearby paths commonly used for farming and grazing without vehicles.
	Distance to a village (m)	DV	The shortest straight-line distance between the

	Distance to farmland (m)	DF	center point of the quadrats and the nearest residential area (villages, city buildings, factory buildings, etc.), measured by GIS. The shortest straight-line distance from the central point of a quadrat to the nearest edge of cultivated land, measured by GIS.
Vegetation factor	Vegetation height of the swamp patch where the roosting site is located in (cm)	VHP	To investigate the average height of perennial herbs in a quadrat in the control sample to obtain the average value from 4 directions and the middle.
	Vegetation height in the roosting area (cm)	VHR	To investigate the average height of perennial herbs in a quadrat in the roosting area, the emergent aquatic plants were also measured. To obtain the average value from the measurements to all plants.
	Vegetation coverage (%)	VC	The proportion of the area of shallow of perennial herbs in total area of a quadrat. Measurement by Braun-Blanquet (Braun-Blanquet et al.1933)
Geographical factor	Nearest distance to surrounding hills (m)	NDH	The shortest straight-line distance between the center point of a quadrat and the edge of the nearest hill, measured by GIS.
	Height of nearest hill (m)	HNH	The relative height of the surrounding nearest hill, measured by GIS.
	Visible angle (°)	(VA)	To calculate the included angle from the location of a quadrat as the angle vertex to two surrounding hills by the lakeshore sides, which were estimated to show the overall openness of the roosting area, measured by GIS.
	Visible range (m <sup>2</sup> )	VR	The area from the center point of a quadrat to the peripheral area with a relative height < 1.2 m, measured by GIS.
	Area of the swamp patch (m <sup>2</sup> )	ASP	The area of the swamp patch where the quadrat is located, measured by GIS.

We conducted sampling quadrats in the roosting area and non-roosting areas for comparison (Fig. 1). We did not set quadrats in the northeastern and northern part of Caohai Lake because there were several docks near the town in Weining County, and even in the swamps in this area black-necked cranes had never appeared for more than ten years (Wu et al. 2020). Quadrat field surveys were conducted intensively for the overwintering population of black-necked cranes in stable periods from December to February of the following year. To avoid disturbing the cranes, we investigated the quadrats after all cranes flew away from the roosting sites to the foraging sites in the morning. We finished at noon before the cranes flew back in the early evening, generally working from 9 am to 1 pm. In the roosting area we set a quadrat within the center of the roosting area. Then on the two sides of the opposite directions of the lakeshore, the following quadrats were set at an interval of 25 m-50 m until outside the roosting area was reached. Seventy-four quadrats with dimensions of 2 m × 2 m in roosting areas were investigated during our study period (3 years), and 74 quadrats (control sampling) in non-roosting areas (with intervals of > 100 m) were surveyed in swamp patches by the lakeshore.

## Data analysis

To test if roost sites were selected relative to non-roost sites, we conducted comparisons of measured variables between these two categories of sites. First, a one-sample Kolmogorov-Smirnov test was used to test each influencing factor's normality. Then, an independent-samples t-test was used to determine if the measurements followed a normal distribution. If data were not normal, we used the Mann-Whitney U test to compare between variables. We regarded statistical significance if  $P < 0.05$ . The variables without any statistical significance were excluded.

The resource selectivity function was developed based on logistic regression to determine factors that varied between roost sites of black-necked cranes and the non roost sites. This information was needed to control the autocorrelations between variables (Lahaye et al. 1999; Wang and Wang 2006). Therefore, we used the Pearson correlation coefficient to test if variables were correlated, and we removed variables with high correlations ( $r > 0.6$ ) to fit the logistic regression model. First, the selected variables were standardized to eliminate the differences generated by different statistical dimensions (Li et al. 2001). Second, the values of the roosting-site quadrats were set as 1, while the control quadrats were set as 0. Then, the backward step method in binomial logistic regression was applied to build the preliminary roosting-site selection model of black-necked cranes. Some variables were excluded through a stepwise conditional check (Pearce and Ferrier 2000). Finally, the receiver operating characteristic curve (ROC) was used to test the efficacy of the model (Boyce et al. 2002).

The resource selectivity function is a linear logarithmic model that includes several independent habitat variables. This model can be used to determine the correlations between variables and the selectivity for each variable (Li et al. 2001). The formula was:

$$w(x) = \exp(\beta_0 + \beta_1x_1 + \beta_2x_2 + \dots + \beta_kx_k)$$

X was the independent variable, and  $\beta$  was the selectivity coefficient.

Then, the roosting-site selection model that indicated the possibility of black-necked cranes choosing a site as the roosting site was built as:

$$P(x) = \frac{\exp(\beta_0 + \beta_1x_1 + \beta_2x_2 + \dots + \beta_kx_k)}{1 + \exp(\beta_0 + \beta_1x_1 + \beta_2x_2 + \dots + \beta_kx_k)}$$

Where  $P(x)=0$  or 1 represented crane nonselection or selection, respectively; the logistic regression coefficient could estimate the selectivity coefficient  $\beta$ . We used SPSS v20 software for

these analyses.

In addition, to compare and determine the selectivity toward the different levels within the same variable, we used Vanderploeg selectivity coefficients ( $W_i$ ) and the Scavia selectivity index ( $E_i$ ) (Vanderploeg et al. 1979) to calculate the preference of black-necked cranes for different levels within a habitat factor, which can also serve as a verification of the roosting-site selection model. The formula was as follows:

$$E_i = (W_i - 1/n) / (W_i + 1/n)$$

$$W_i = (r_i/p_i) / \sum (r_i/p_i)$$

In the formulas,  $n$  is the number of ecofactor traits;  $P_i$  refers to the number of quadrats with trait  $i$ ; and  $r_i$  means the number of quadrats with trait  $i$  that the black-necked cranes chose the farming area.  $E_i = -1$  represents no choice;  $-1 < E_i < 0$  represents a tendency to avoid;  $E_i = 0$  or approaching 0 represents a random choice;  $0 < E_i < 1$  represents a positive choice and  $E_i = 1$  represents a highly positive choice (Wu et al. 2020).

The criteria for statistically significant differences were as follows: extremely significant difference ( $P < 0.01$ ), significant difference ( $P < 0.05$ ), and no significant difference ( $P > 0.05$ ). The correlation ratings were extremely strong correlation ( $0.8 < r \leq 1.0$ ), strong correlation ( $0.6 < r \leq 0.8$ ), medium correlation ( $0.4 < r \leq 0.6$ ), minimal correlation ( $0.2 < r \leq 0.4$ ), and minimum or no correlation ( $0.0 < r \leq 0.2$ ) (Lahaye et al. 1999).

## RESULTS

### Influencing factors on roost site selection by black-necked cranes

Comparisons between study quadrats and control quadrats for all 14 habitat factors showed that 13 habitat factors had significant differences ( $P < 0.05$ ) except vegetation coverage (VC;  $P = 0.21$ ), which indicated that characteristics of black-necked crane roost sites were significantly different from characteristics at control sites. And several variables showed highly significant differences (Table 2).

**Table 2.** Significance test on influencing factors between the study quadrats and control quadrats

Factors	Study quadrats	Control quadrats	t-test	Mann-Whitney U
WD (cm)	12.87 ± 7.39	21.11 ± 12.05	-	0.00**
DMR (m)	900.84 ± 246.75	1009.81 ± 338.81	-	0.03*
DTR (m)	518.19 ± 165.04	440.15 ± 192.94	-	0.01*
DP (m)	307.80 ± 129.19	174.92 ± 91.15	-	0.00**
DV (m)	545.58 ± 157.92	323.66 ± 158.68	-	0.00**
DF (m)	431.59 ± 168.42	181.22 ± 105.46	0.00**	-
VHP (cm)	46.40 ± 37.38	34.11 ± 38.39	-	0.00**
VHR (cm)	5.32 ± 7.13	29.31 ± 35.77	0.00**	-
VC (%)	0.35 ± 0.25	0.42 ± 0.25	-	0.21
NDH (m)	484.14 ± 175.49	226.97 ± 125.90	0.00**	-
HNH (m)	20.91 ± 10.73	44.32 ± 25.13	0.00**	-
VA (°)	117.22 ± 61.88	156.11 ± 38.96	0.00**	-
VR (m <sup>2</sup> )	1016000.43 ± 745010.10	231899.68 ± 250972.40	0.00**	-
ASP (m <sup>2</sup> )	260725.73 ± 181178.55	73811.48 ± 54581.50	0.00**	-

Notes: \* $P < 0.05$ ; \*\* $P < 0.01$ , see table 1 for the abbreviations of the variables.

### Roost site selection by black-necked cranes

Correlation analysis indicated that among these factors (Table 3), the following factors showed strong correlations ( $r > 0.6$ ) with each other: VA and DTR ( $r = -0.606$ ), VA and VR ( $r = -0.692$ ), DV and NDH ( $r = 0.861$ ), DV and DF ( $r = 0.799$ ), DV and DP ( $r = 0.639$ ), DV and ASP ( $r = 0.647$ ), NDH and DF ( $r = 0.739$ ), NDH and DP ( $r = 0.819$ ), ASP and DP ( $r = 0.683$ ), ASP and DF ( $r = 0.737$ ), ASP and NDH ( $r = 0.744$ ), and ASP and VR ( $r = 0.684$ ).

**Table 3.** Correlation analysis of habitat factors (variables)

Variables	RD (m)	CD (m)	PD (m)	VD (m)	FD (m)	MD (m)	MH (m)	AM (°)	SH (cm)	VH (cm)	VC (%)	SD (cm)	VA (m <sup>2</sup> )	PA (m <sup>2</sup> )
DMR (m)	1													
DTR (m)	0.292	1												
DP (m)	-0.095	0.506	1											
DV (m)	-0.113	0.331	<b>0.639</b>	1										
DF (m)	-0.053	0.226	0.564	<b>0.799</b>	1									
NDH (m)	-0.112	0.357	<b>0.739</b>	<b>0.861</b>	<b>0.819</b>	1								
HNH (m)	-0.107	-0.350	-0.278	-0.281	-0.259	-0.315	1							
VA (°)	-0.102	<b>-0.606</b>	-0.600	-0.522	-0.348	-0.542	0.430	1						
VHP (cm)	0.07	-0.032	0.180	-0.02	0.073	0.12	0.068	0.086	1					
VHR (cm)	0.177	-0.191	-0.175	-0.317	-0.300	-0.283	0.223	0.15	0.535	1				
VC (%)	0.177	-0.116	-0.02	-0.033	0.034	0.025	0.172	0.12	0.230	0.468	1			
WD (cm)	0.225	0.044	-0.238	-0.196	-0.284	-0.298	0.197	0.004	-0.199	0.206	0.058	1		
VR (m <sup>2</sup> )	-0.289	0.391	0.580	0.568	0.459	0.592	-0.476	<b>-0.692</b>	-0.095	-0.260	-0.124	-0.087	1	
ASP (m <sup>2</sup> )	-0.213	0.322	<b>0.683</b>	<b>0.647</b>	<b>0.737</b>	<b>0.744</b>	-0.328	-0.417	0.129	-0.157	0.077	-0.313	<b>0.684</b>	1

\*See Table 1 for the abbreviations of the variables.

According to the correlations and the information on the Caohai wetland, the redundant factors could be excluded for logistic regression model fitting, including VC, DF, DP, NPH, VA, and ASP. Then, we analyzed eight independent ( $r \leq 0.6$ ) influencing factors on the roosting sites of black-necked cranes. Finally, only four factors, including VHP ( $\beta = 8.397$ ), VHR ( $\beta = -7.999$ ), HNH ( $\beta = -4.105$ ), and VR ( $\beta = 1.584$ ), were used in the logistic regression formula according to the results of the test (Table 4). Therefore, the roosting-site selection model was determined to be

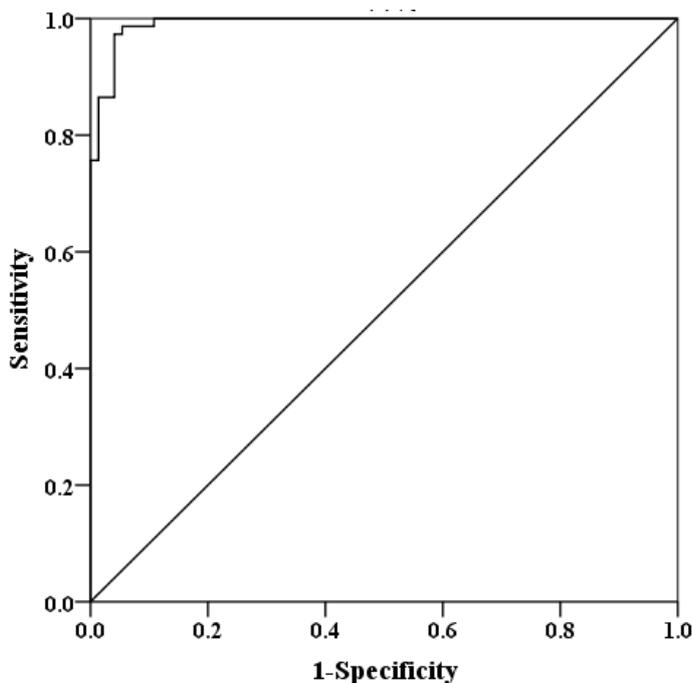
$$P = e^{\text{Logit}(p)} / (1 + e^{\text{Logit}(p)}), \text{Logit}(p) = 1.243 + 8.397\text{VHP} - 7.999\text{VHR} - 4.105\text{HNH} + 1.584\text{VR}.$$

The ROC curve testing of this formula showed that the area under the curve for this model reached 99.2%, which indicated that the regression formula had a high ability to differentiate roost sites further suggesting that the chosen variables were important in influencing roost site selection (Fig. 2).

**Table 4.** Selectivity coefficient of variables for the model of roosting-site selection by black-necked cranes

Factors	Regression coefficient ( $\beta \pm \text{SE}$ )	Chi-square test value	Significance (P)
Z -HNH	-4.105 $\pm$ 1.693	5.879	0.015
Z -VHP	8.397 $\pm$ 2.163	15.075	0.000
Z -VHR	-7.999 $\pm$ 2.039	15.389	0.000
Z -VR	1.584 $\pm$ 0.704	5.070	0.024
Z -Constant	1.243 $\pm$ 0.788	2.489	0.115

Notes: Z- standardization, HNH- height of nearest hill (m), VHP- vegetation height of the swamp patch where the roosting site is located (cm), VHR- vegetation height in the roosting area (cm), and VR- visible range (m<sup>2</sup>). The formula classification performance reached 95.2%, and the effectiveness of the formula was tested by the Chi-square test:  $\chi^2 = 170.22$ ,  $P = 0.000$ .



**Fig. 2.** The test results of the ROC curve. Note: the diagonal represents that the model had no judgment ability (50% area and below), while above the diagonal represents that the model had judgment ability (50% or above).

**Selectivity to levels within the main influencing factors**

The results of the Vanderploeg selectivity coefficients ( $W_i$ ) and Scavia selectivity index ( $E_i$ ) in terms of the eight main factors were as follows (see Table 5): cranes preferred to choose the swamp area with minimal human disturbance (the DMR > 1300 m ( $E_i = 0.602$ ), DV > 650 m ( $E_i = 0.662$ ), DTR > 500 m ( $E_i = 0.469$ )), a vast area (HNH < 15 m ( $E_i = 0.589$ ), VR > 550000 m<sup>2</sup> ( $E_i = 0.297$ )), low vegetation height (VHR < 5 cm ( $E_i = 0.293$ ), VHP in 35 cm–60 cm ( $E_i = 0.595$ )), and shallow water (WD < 5 cm ( $E_i = 0.449$ )) to roost overnight.

**Table 5.** Selectivity of black-necked cranes for roosting sites using Vanderploeg selectivity coefficients ( $W_i$ ) and Scavia selectivity index ( $E_i$ )

Variables	i	P <sub>i</sub>	A <sub>i</sub>	φ <sub>i</sub>	W <sub>i</sub>	E <sub>i</sub>
DMR (m)	< 300	0.014	0.054	0.250	0.013	-0.833
	300–500	0.014	0.054	0.250	0.013	-0.833
	500–700	0.095	0.095	1.000	0.052	-0.465
	700–900	0.189	0.216	0.875	0.046	-0.515
	900–1100	0.338	0.486	0.694	0.036	-0.595
	1100–1300	0.162	0.122	1.333	0.070	-0.345
	> 1300	0.149	0.014	11.000	0.574	<b>0.602</b>
DV (m)	< 150	0.014	0.122	0.111	0.006	-0.916
	150–250	0.041	0.270	0.150	0.008	-0.889
	250–350	0.068	0.243	0.278	0.016	-0.803
	350–450	0.216	0.162	1.333	0.075	-0.313
	450–550	0.081	0.068	1.200	0.067	-0.359
	550–650	0.243	0.108	2.250	0.126	-0.062
	> 650	0.338	0.027	12.500	0.701	<b>0.662</b>
DTR (m)	< 100	0.014	0.041	0.333	0.107	-0.303
	100–300	0.095	0.203	0.467	0.150	-0.144
	300–500	0.216	0.365	0.593	0.190	-0.025
	> 500	0.676	0.392	1.724	0.553	<b>0.469</b>
	VHP (cm)	< 5	0.027	0.135	0.200	0.034
VHR (cm)	5–15	0.054	0.203	0.267	0.045	-0.571
	15–25	0.162	0.135	1.200	0.205	0.103
	25–35	0.419	0.270	1.550	0.264	0.227
	35–60	0.176	0.122	1.444	0.657	<b>0.595</b>
	> 60	0.162	0.135	1.200	0.205	0.103
WD (cm)	< 5	0.595	0.270	2.200	0.458	<b>0.293</b>
	5–15	0.311	0.149	2.091	0.435	0.270
	15–24	0.068	0.149	0.455	0.095	-0.451
	> 24	0.027	0.432	0.063	0.013	-0.901
VR (m <sup>2</sup> )	< 5	0.230	0.054	4.250	0.526	<b>0.449</b>
	5–10	0.216	0.135	1.600	0.198	-0.005
	10–15	0.149	0.162	0.917	0.113	-0.276
	15–20	0.257	0.284	0.905	0.112	-0.282
	> 20	0.149	0.365	0.407	0.050	-0.597
HNH (m)	< 300000	0.243	0.838	0.290	0.014	-0.869
	300000–400000	0.095	0.027	3.500	0.169	-0.084
	400000–550000	0.162	0.068	2.400	0.116	-0.266
	550000–750000	0.095	0.014	7.000	0.338	<b>0.257</b>
	> 750000	0.405	0.054	7.500	0.362	0.091
VHR (cm)	< 15	0.311	0.014	23.000	0.773	0.589
	15–20	0.311	0.054	5.750	0.193	-0.017
	20–25	0.014	0.095	0.143	0.005	-0.953
	25–30	0.149	0.392	0.379	0.013	-0.880
	> 30	0.216	0.446	0.485	0.016	-0.849

\*See Table 1 for the abbreviations of the variables, I: gradients of a variable, P<sub>i</sub>: used proportion, A<sub>i</sub>: expected proportion, φ<sub>i</sub> = P<sub>i</sub>/A<sub>i</sub>, W<sub>i</sub>: selectivity coefficient, and E<sub>i</sub>: selectivity index.

## DISCUSSION

### Factors influencing the selection of roosting sites by black-necked cranes

According to the roosting-site selection model we obtained, the most important influencing factors included: (1) the vegetation height of the swamp patch where the roosting site was located (VHP;  $\beta = 8.397$ ), which suggests that cranes prefer sites with good vegetation cover. (2) The vegetation height in the roosting area (VHR) ( $\beta = -7.999$ ) was negatively related to a crane's choice. Black-necked cranes prefer to choose places with lower vegetation heights, relative to control sites, for roosting. This may be a function of the large body size of cranes who cannot easily take off (Lu et al. 2017). If cranes wanted to take off rapidly at short notice, they jump and flap their wings quickly for vertical takeoff (Lu et al. 2017; Hoyo et al. 1996). Therefore, very tall vegetation would be a hindrance. 3) The height of the nearest hill (HNN) ( $\beta = -4.105$ ), and 4) the visible range (VR) ( $\beta = 1.584$ ) showed that black-necked cranes preferred to choose places that were flat with a broad area in the lakeshore area. These findings are similar to the results for the Dashanbao wetland, another important overwintering site of black-necked cranes in Yunnan Province (Li et al. 2018). In summary, geographic factors and vegetation factors appear to be primary factors that influence black-necked cranes' selection of roost sites. Comparatively, the interference factors did not serve as the main influencing factors, perhaps because human activities often occurred far away from the roosting area and not in the swamp patches of the lakeshore (Zhang et al. 2019).

### How black-necked cranes select a roosting site in the Caohai wetland

Although the resource selectivity function and roosting-site selection model could systematically analyze wild animal selectivity of various habitat variables, as well as consider the combined effects of these variables (Wang and Wang 2006), the functions treated all habitat factors equally, so the model could not compare or rank the selectivity of different gradients in a habitat factor (Yang et al. 2006). For this reason, we used the selectivity coefficients and selectivity index (Vanderploeg and Scavia 1979) to analyze the selection preference of black-necked cranes for different levels of primary habitat factors as a complement to the roosting-site selection model.

According to the selectivity coefficients and selectivity index (Table 5), the black-necked cranes selected roost sites in the Caohai wetland that primarily avoided human disturbances, such as villages/settlements and roads. Therefore, the most suitable areas were >1300 m from main roads, the distance to villages/residential area was > 650 m and the distance to rural/tractor roads was >

500 m. In terms of geographical factors, the black-necked cranes preferred the relatively open area with the surrounding mountain height of  $< 15$  cm and a visible range of  $> 550000$  m<sup>2</sup>, which the roosting-site selection model also verified. The black-necked cranes preferred to roost in the shallow swamp area with a water depth  $< 5$  cm and a vegetation height  $< 15$  cm. Other studies have reported that swamps, marshes, and shallow water habitats are essential habitats for black-necked crane roosting but have not evaluated selection (Li et al. 2005; Liu et al. 2008; He et al. 2011). Similarly, the red-Crowned crane (*Grus japonensis*), Siberian crane (*Grus leucogeranus*), Sandhill crane (*Grus canadensis*), Common crane (*Grus grus*), and other crane species have also been found to roost in wetlands, such as manufactured wetlands, shallow lakes, rivers, ponds, and reservoirs (Folk and Tacha 1990; Avilés 2004; Wu 2005; Pearse et al. 2017; Wang et al. 2019), but very few studies have examined whether these roost sites are preferentially selected due to specific variables wetlands (He et al. 2011).

He et al. (2011) discussed that the black-necked cranes choose shallow water swamps as roosting sites to save energy and reduce heat loss. Due to the relatively broad environment of the lakeshore, we assumed that energy savings and heat loss were not the main influencing factors, but that human disturbance would primarily lead to cranes selecting roost sites. When there is extremely high pressure from human disturbance or habitat loss, black-necked cranes may be forced to abandon swamps, even wetlands, as roosting sites. An extreme case was reported for the Huize wetland and Yongshan wetland, both in Yunnan Province, where the black-necked cranes were found roosting on the hillsides near the lakes because their roosting sites on the lakeshore disappeared and were heavily disturbed by humans (Wu et al. 2013; Lu et al. 2017). The microenvironment of the hillside may be more helpful to cranes for energy conservation and heat loss reduction, but this is not normal for cranes. According to our results, we suggest that the habitat patches in the Caohai wetland are appropriately managed, and extreme cases such as Huizhe and Yongshan are avoided in Caohai or other wetlands where black-necked cranes overwinter.

## CONCLUSIONS

Based on the above results, as summarized below: (1), Geographic factors and vegetation factors appear to be the main factors influencing black-necked cranes' selection of roost sites at Caohai; (2), The black-necked cranes roosting sites in the Caohai wetland were much further away from human disturbances, such as villages/settlements and roads, relative to control sites; (3), Energy savings and heat loss were unlikely to be the main influencing factors leading to roost site selection.

We first gathered data about black-necked crane selection of roosting sites in a highly complex wetland system. Based on the current study's finding, we strongly recommend appropriately managing Caohai wetlands, which will have implications for the conservation management of overwintering of black-necked cranes in wetlands.

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**Authors' contributions:** GX, SH, ZY and SX conceived the study; GX, HC, SX and ZY analyzed the data; GX, ZY and SH wrote the manuscript. HS and RHK supervised the research and provided multiple revisions of the writing. CH conducted research method guidance for the article. MZ and XS implemented the field surveys and collected the data. All authors read and approved the final manuscript.

**Competing interests:** The authors have no competing interests.

**Availability of data and material:** The datasets generated and/or analyzed during the current study are available from the corresponding author upon reasonable request.

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**Supplementary materials**

**Fig. S1.** Black-necked Crane in their roosting sites in Caohai, photoed in early morning.

(download)

**Fig. S2.** Black-necked in non-roosting-site, Caohai wetland. (download)

**Fig. S3.** Swamp near the village. (download)

**Fig. S4.** View of lakeshore, the opposite is near the Weining County town. (download)