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Seasonal Migration and Daily Movement Patterns of Sympatric Overwintering Black-necked Cranes (*Grus nigricollis*) and Common Cranes (*Grus grus*) in Caohai, Guizhou, China

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Abstract.—Wintering Black-necked (*Grus nigricollis*) and Common (*G. grus*) cranes occur sympatrically in Caohai Wetland, Guizhou, China. Seasonal migration dynamics, daily movement patterns, and diurnal activity budgets of the two crane species were investigated in Caohai Wetland, in order to characterize their wintering activity differences and the mechanism of interspecific coexistence, during October - April 2014 - 2017. Black-necked Cranes wintered in Caohai for 147 ± 8 days, and Common Cranes for 169 ± 8 days. Common Cranes generally arrived in Caohai 11.4 ± 3.28 days earlier and departed 11.00 ± 3.20 days later than Black-necked Cranes. During winter in Caohai Wetland, the behavioral activities of both the Black-necked and Common cranes were strongly influenced by circadian rhythms. However, there were significant differences in daily temporal patterns between them in percent time spent in specific behaviors. Common Cranes left their roosting sites 20 min. earlier than Black-necked Cranes and returned 32 min. later. Common Cranes also spent more time foraging and being vigilant than Black-necked Cranes. *Received 24 May 2021, accepted 6 July 2021.*

Key words.—Behavior, Black-necked Crane, China, Common Crane, Caohai Wetland, daily movement, foraging, migration, roost.

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Niche separation and interspecific competition is a critical issue in explaining patterns of coexistence of wildlife, which is of broad interest to ecologists. There are many hypotheses that attempt to understand the mechanisms of niche separation (Schreier *et al.* 2009; Bagchi *et al.* 2003), including spatial and temporal differences in behaviors, resource partitioning, and habitat separation. Seasonal migration dynamics, daily movement patterns, and time budgets are important foci for bird behavior research (Fronczak *et al.* 2017; Krapu *et al.* 2015). Food resources and environmental factors vary with time and habitat (Henry and Cumming 2016; Zhang *et al.* 2015), and many birds cope with annual fluctuations in environmental conditions by seasonal migration, which strongly impacts their reproduction and life histories (Mi *et al.* 2018). Studies of bird behavior can increase our understanding of bird biology, including their physiological and ecological requirements (Lonsdorf *et al.* 2016).

Black-necked (*Grus nigricollis*) and Common (*G. grus*) cranes are evolutionarily closely related species and have similar body size and diet (Krajewski *et al.* 2010). Black-necked Cranes are the only crane (Gruidae) species that inhabits and reproduces in the freshwater wetlands of high plateaus (2500-5000 m.a.s.l.), mainly distributed in the Qinghai-Tibet Plateau and Yunnan-Guizhou Plateau. It has a global population of 10,000 - 10,200 individuals (Li *et al.* 2014) and is considered vulnerable according to the IUCN Red List (Birdlife 2020), due to threats from climate change, habitat destruction, and human interference (Liu *et al.* 2010). Comparatively, Common Crane has the broadest range in Eurasia of all crane species and has a global population of 491,000-503,000 individuals. It is listed as Least Concern by IUCN (Birdlife 2020).

Black-necked and Common cranes winter sympatrically in many wetlands in the Yunnan-Guizhou Plateau, including the Dashanbao Nature Reserve, the Huize Nature Reserve, and the Napa Lake Nature Reserve in Yunnan province, as well as the Caohai Nature Reserve in Guizhou province (Li *et al.* 2014). Populations of winter-

ing Black-necked and Common cranes are largest in Caohai Wetland, where the typical competitive coexistent relationship between the two species can be observed (Li 2003), as they share the same roosting and foraging sites around Caohai Wetland. Wintering Black-necked and Common cranes immigrate asynchronously to the Caohai Wetland during September and October and emigrate from Caohai Wetland during March and April of the following year (Wu 1985).

The spatial distribution of roosting and foraging sites of the two species overlap around Caohai Wetland, though they aggregate by species and keep some distance between the species (Sun *et al.* 2018). They leave the roosting sites before dawn to foraging sites and return to roosting sites before sunset (Sun *et al.* 2018), and the daily movement of the two species are often affected by temperature (Song *et al.* 2014). However, there are noticeable differences between the diurnal activity budgets of the two species. We surveyed the seasonal migration dynamics, daily movement patterns, and diurnal activity budgets of sympatric wintering Black-necked and Common cranes in Caohai Wetland to characterize their wintering diurnal activity patterns and identify differences between the two species to begin to understand the mechanisms allowing interspecific coexistence.

METHODS

Study Area

The Caohai Wetland (26° 47′ - 26° 52′ N, 104° 10′ - 104° 20′ E) is located in the central part of Weining County, Guizhou Province, China. As the largest natural freshwater lake in Guizhou, it has a large area of 120 km^2, with 25 km^2 covered by water and a mean water depth of 1.35 m (Wu *et al.* 2020; Xu *et al.* 2015). The Caohai Wetland is a shallow lake surrounded by large amounts of cultivated land, with large beaches and abundant aquatic plant communities, formed by its unique geological, climatic, and cultural characteristics (Song *et al.* 2014). Therefore, it supplies natural habitat for the roosting and foraging of > 80 wading bird species, with a total population > 80,000 individuals (Li *et al.* 2014; Wu *et al.* 2020). The Caohai Nature Reserve was established as a provincial-level reserve in 1985 and was upgraded to a national-level reserve in 1992 to protect the waterbirds and the plateau wetland ecosystem (Xu *et al.* 2015). The Caohai Wetland is considered an important wintering habitat for Black-necked and Common cranes (Song *et al.* 2014), and the number of wintering Black-necked Cranes increased from 223 in 1983 to more than 2,000 in 2016 (Ran *et al.* 2017), due to conservation efforts. For many years, Black-necked and Common cranes (hereafter cranes) have used seven major roosting sites in Caohai Wetland: Liujiaxiang, Wangjiayuanzi, Huyelin, Wenjiatun, Yangguanshan, and Jiangjiawan (Fig. 1). The foraging sites of both species are widely distributed within the Caohai wetland and surrounding regions, primarily in cultivated land, shallow swamps, and grasslands (Sun *et al.* 2018).

Survey of the Seasonal Migration

We surveyed the annual arrival dates to and departure dates from the Caohai Wetland for Black-necked and Common cranes, and counted them, between 2012 and 2017. For understanding the effect of temperature on the Black-headed and Common crane's migration, we recorded the daily maximum and daily minimum temperature everyday during the migration seasons (October-November and March-April). According to the population dynamics of wintering cranes from the beginning of immigration to Caohai to the end of emigration from Caohai, there are three different periods characterized by increasing, stable and decreasing population size, here called the immigration phase (from the date of first sighting to the date of population stability), stability phase (from the date of population stability to the date of first departure), and the emigration phase (from the date of first departure to the date of last sighting).

Survey of Daily Movement Patterns

We observed and recorded the time and numbers of Black-necked and Common cranes when they left roosting sites for foraging sites in the morning (06:00-08:00), and returned to roosting sites at dusk (18:00-20:00) every survey day from October 2016 to March 2017. Observations were carried out with the aid of binoculars (Swarovski Pocket 10 × 25b) and a spotting scope (Swarovski-Sts 65 hd) at the 7 roosting sites used by both species. We also recorded environmental parameters including temperature, humidity, precipitation, time of sunrise and sunset, using the portable automatic weather station (Delta-T, WS-GP2). A total of 59 days of leaving roosting sites and 55 days of returning were surveyed.

Survey of Diurnal Activity Budgets

Diurnal activity budgets were measured by searching for and observing flocks of cranes from 08:00-18:00 each day. Focal groups of cranes were scanned every 5 min to record instantaneous behavior of each visible individual in the flock. Flocks were observed in this manner until they left the visual field, at which time we found another flock for behavior observation. Eight categories of behavior common to both species (Yang *et al.* 2007) were recorded during each scan sample (Table 1). We used the percentage of individuals in

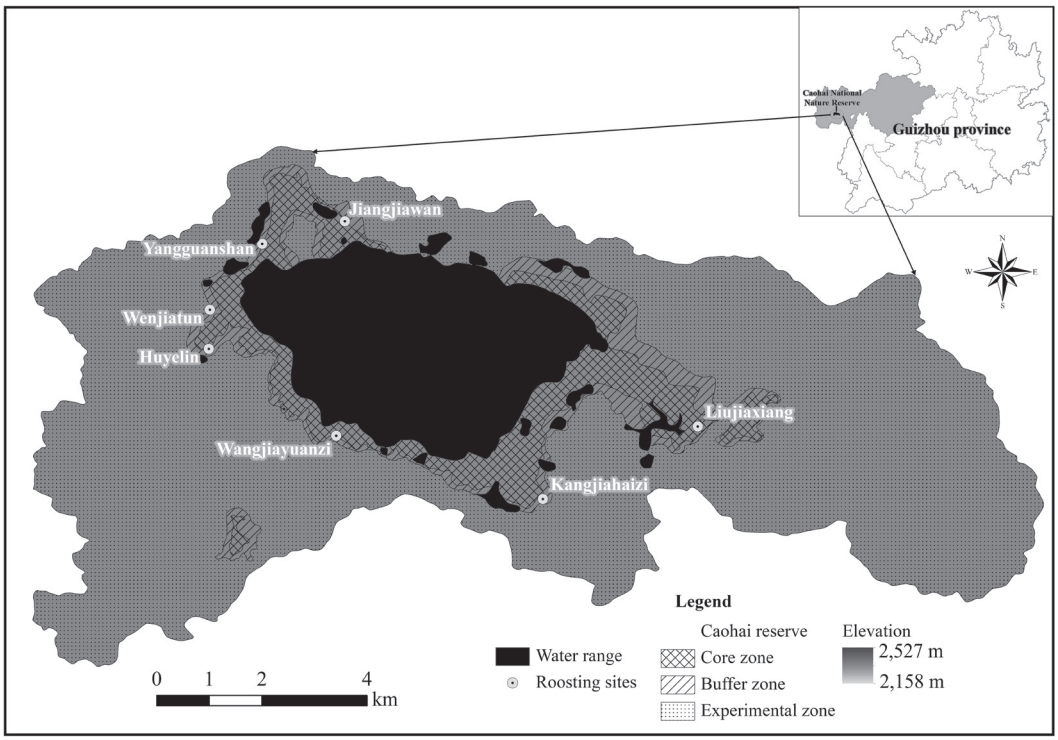

Figure 1. Location of Caohai National Nature Reserve Wetland, Guizhou, China (inset) and winter communal roost sites of Black-necked (*Grus nigricollis*) and Common (*G. grus*) cranes within the reserve.

each behavioral category recorded in scans to calculate the average % time spent in each activity for each hour of observation (Zhou *et al.* 2010).

Statistical Analysis

We recorded the time of first departure from roost for each species each day, and compared the average time of first departure between species using a Mann Whitney U test (Pickens 2017). We did likewise for time of arrival at roosts in the evening. We used Chi Square test to test the difference of diurnal activity budgets between Black-necked and Common cranes. Statistical analyses were performed with IBM SPSS Statistics 22.0, and Origin 8.0 (Wu *et al.* 2020).

RESULTS

Temporal Migration Patterns in Winter

Black-necked Cranes arrived in Caohai Wetland to over-winter between mid-October and early November (median arrival

Table 1. The behavioral categories of Black-necked (*Grus nigricollis*) and Common (*Grus grus*) cranes wintering in Caohai Wetland, Guizhou, China.

Behavior	Description
Foraging	Foraging-related processes, such as searching, collecting food, pecking, and swallowing
Locomotion	Short-distance non-foraging movements and searching
Preening	Using beak to repeatedly comb feathers
Resting	Standing still upright with head buried in back feathers; standing still on one or two legs; squatting or lying in dry places
Agonism	Ritual threats and direct fighting, using beaks or wings to attack other individuals of the same species or individuals of other species
Vigilance	Releasing a warning cry; looking around, neck extended; moving around and looking up; standing still and looking into the distance
Flying	Long- or short-distance flying or gliding
Others	Dancing, chasing, drinking water, singing, bathing, flapping, etc.

date = 31 October), stayed for a mean duration of 147.00 ± 8.00 days (range: 132-161 days), and departed by the end of following March (median departure date = 30 March) (Fig. 2). Comparatively, Common Cranes arrived in Caohai wetland in mid-late October (median arrival date = 20 October), stayed for a mean duration of 169.40 ± 8.08 days (range: 160-183 days), and departed by the beginning of the next April (median departure date = 8 April) (Fig. 2). Common Cranes arrived 11.40 ± 3.28 days earlier and departed 11.00 ± 3.20 days later than Black-necked Cranes (Table 2).

During the wintering period of 2015-2016, Black-necked Cranes stayed 153 days in Caohai, while Common Cranes stayed 176 days, and 1,537 Black-necked Cranes immigrated to Caohai Wetland from 29 Oct to 28 Nov 2015 (30 days), accounting for 67% of the total wintering population. Numbers are mean ± SE. The peak number of Black-necked Cranes (mean = 1,804.61 ± 264.06 individuals) remained stable from 29 November 2015 to 5 March 2016 (98 days). Black-necked Cranes emigrated from Caohai Wetland during 6 March to 30 March 2016 (25 days) (Fig. 2).

Comparatively, the numbers of Common Cranes took a longer time to reach stability than that of Black-necked Cranes, from 23 October to 5 December 2015 (43 days), and the peak number of Common Cranes (mean = 829.93 ± 173.12 individuals) remained stable from 6 December 2015 to 27 February

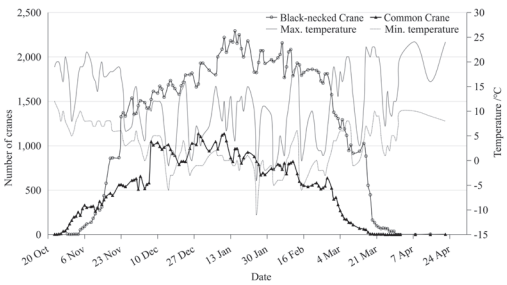

Figure 2. Fall migration arrival, peak numbers, and spring migration departure of wintering Black-necked (*Grus nigricollis*) and Common (*G. grus*) cranes during Oct 2015-Apr 2016 in Caohai Wetland, Caohai National, Nature Reserve, China.

Table 2. Temporal migration dynamics of Black-necked (*Grus nigricollis*) and Common (*Grus grus*) cranes wintering in Caohai Wetland, Guizhou, China.

	Earliest arrival time				Latest departure time			Wintering days (day)	
Year	Black-necked Crane	Common Crane	Interval (day)	Year	Black-necked Crane	Common Crane	Interval (day)	Black-necked Crane	Common Crane
2012	18 Oct	9 Oct	9	2013	28 Mar	10 Apr	13	161	183
2013	5 Nov	23 Oct	13	2014	29 Mar	3 Apr	5	144	162
2014	8 Nov	21 Oct	18	2015	20 Mar	30 Mar	10	132	160
2015	29 Oct	23 Oct	6	2016	30 Mar	16 Apr	17	153	176
2016	4 Nov	24 Oct	11	2017	29 Mar	8 Apr	10	145	166
Mean ± SD			11.40 ± 3.28		——		11.00 ± 3.20	147.00 ± 8.00	169.40 ± 8.08

2016 (98 days). Common Cranes emigrated from Caohai Wetland from 28 February to 16 April 2016 (49 days) (Fig. 2).

Daily Roost Departure and Arrival

Black-necked Cranes left their roosting sites at about 07:42 in the morning, while Common Cranes left at about 07:22. Common Cranes left their roosting sites an average of 20 ± 5 min (numbers are mean ± SE) earlier than Black-necked Cranes. Black-necked and Common cranes returned to their roosting sites at about 18:10 and 18:42 at dusk, respectively. Therefore, Common Cranes returned to their roosting sites an average of 32 ± 8 min later than Black-necked Cranes. Black-necked Cranes spent an average of 10 hr 28 min (± 20 min) away from the roosting sites, while Common Cranes spent an average of 11 hr 20 min (± 25 min). Thus, Common Cranes stayed approximately 52 min longer at their foraging sites than the Black-necked Cranes. The result of Mann-Whitney U test showed that the time of leaving from and returning to the roosting sites significantly differed between the two species ($U = 87$, df = 34, $n = 35$, $P < 0.01$). For both species, the time of departure from roosts and arrival at roosts was correlated with sunrise and sunset, respectively. Black-necked Cranes left roosting sites at about 8 ± 3 min after sunrise (Fig. 3) and returned to roosting sites at about 30 ± 20 min before sunset (Fig. 4). Common Cranes left roosting sites at about 12 ± 8 min before sunrise (Fig. 3) and returned to roosting sites at about 16 ± 8 min after sunset (Fig. 4).

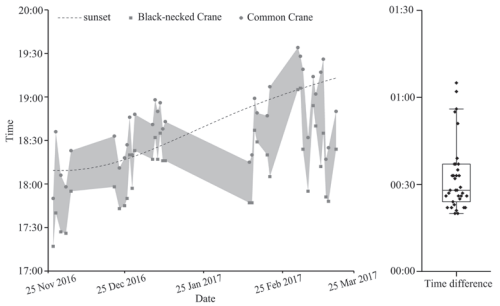

Figure 4. Time of arrival to roosting sites of wintering Black-necked (*Grus nigricollis*) and Common (*G. grus*) cranes in Caohai Wetland, Caohai National Nature Reserve, Guizhou, China.

Diurnal Activity Budgets

Diurnal time budgets were similar between Black-necked and Common cranes with regard to dominant daily behaviors (Fig. 5). They both spent most of their time foraging (47.55 ± 6.14% for Black-necked Crane and 50.36 ± 3.75% for Common Crane), numbers are mean percentage ± SE., followed by vigilance (15.36 ± 1.63% and 18.64 ± 2.46%, respectively) and foraging-related locomotion (10.91 ± 4.61% and 11.00 ± 3.16%, respectively). Resting and preening were less commonly observed in both species (Fig. 5). There were two daily time-periods with a high frequency of forag-

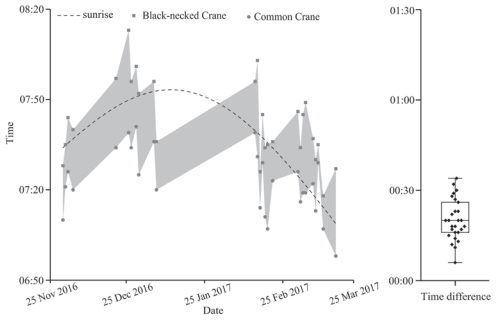

Figure 3. Time of departure from roosting sites of wintering Black-necked (*Grus nigricollis*) and Common (*G. grus*) cranes in Caohai Wetland, Caohai National Nature Reserve, Guizhou, China.

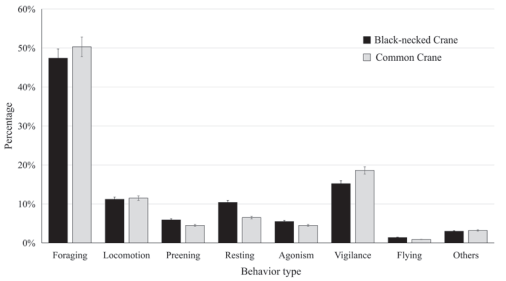

Figure 5. Daily percentage of behavioral activities of wintering Black-necked (*Grus nigricollis*) and Common (*G. grus*) cranes in Caohai Wetland, Caohai National Nature Reserve, Guizhou, China.

ing observed in Black-necked Cranes (10:00-12:00 and 16:00-18:00), and three time-periods with high frequency of foraging observed in Common Cranes (9:00-10:00, 13:00-14:00 and 17:00-18:00). Other behaviors such as resting, preening, and vigilance occurred intermittently during foraging time-periods (Figs. 6, 7). Common Cranes spent more of their time foraging and more time vigilant than Black-necked Cranes (Figs. 6, 7), but there were no significant differences in the time budgets of the two species.

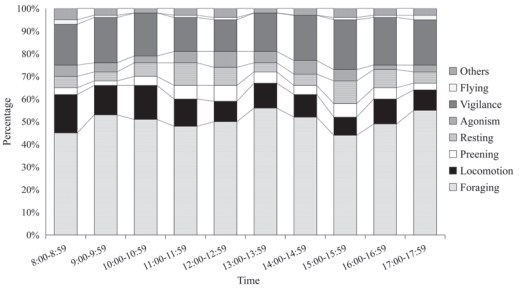

Figure 7. The diurnal activity budget of wintering Common Crane (*Grus grus*) in Caohai Wetland, Caohai National Nature Reserve, Guizhou, China.

DISCUSSION

Sympatric species should reduce competition by selecting different habitat and food, and by having different activity timing, especially when they have similar niches (Schreier *et al.* 2009). Black-necked and Common cranes occur sympatrically in many wetlands during wintering seasons, and they were found to have similar wintering ecology (Wang *et al.* 2018). Kong *et al.* (2018) reported that wintering Black-necked and Common cranes occurring sympatrically in Huize Nature Reserve, Yunnan, have communal nightly roosting sites and separate daily foraging sites, affected by the interspecies competition. Black-necked and Common cranes share the same roosting and foraging sites around Caohai Wetland, but they aggregate by species and keep some distance between them (Sun *et al.* 2018).

We found differences in seasonal migration dynamics (arrival and departure) and overwintering movement patterns between the sympatric wintering Black-necked and Common cranes in Caohai Wetland. The interspecific differences in migration timing are likely due to the relative locations of the breeding grounds of the two species. The breeding grounds of Common Crane are higher in latitude (Wang and Wang 2003), and autumn temperatures at the breeding grounds decrease earlier and faster. Thus, Common Cranes tend to migrate to the Caohai Wetland earlier than Black-necked Cranes and depart later, presumably because temperatures in their breeding grounds warm more slowly and later in spring.

The number of days from first arrival to maximum or stable number was less for Black-necked Cranes than for Common Cranes. This phenomenon is likely related to the difference of the spatial distribution of the breeding grounds of Black-necked Cranes and Common cranes. The Black-necked Cranes wintering in Caohai are part of the migratory population of the eastern flyway (Ruoergai-Yunnan and Guizhou Flyway), and mainly originate from the Greater Ruoergai wetland area in Sichuan Province, China (Kong *et al.* 2014), with their breeding grounds concentrated in a relatively small area and their population aggregation high during migration. However, the breeding grounds of Common Cranes are spread throughout northern Eurasia, with a broad distribution in Xinjiang as well as northeast, northwest, and eastern China. They have a larger range and more dispersed population than Black-necked Cranes. The migrating populations of Common Crane in China are

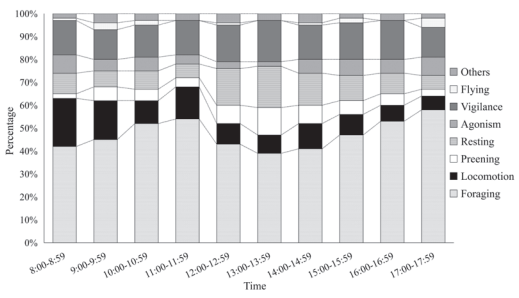

Figure 6. The diurnal activity budget of wintering Black-necked Crane (*Grus nigricollis*) in Caohai Wetland, Caohai National Nature Reserve, Guizhou, China.

divided into Eastern China Flyway, Central China Flyway, and Western China Flyway populations (Song *et al.* 1998), and the wintering populations in Caohai mainly belong to the western flyway population, originating in Xinjiang, Gansu, and western Europe (Wang and Wang 2003).

During winter, bird daily movements and diurnal activity budgets are related to metabolic energy demands (Jorgensen and Brown 2017), which are affected by food abundance, temperature, individual physiology, and human interference (Tatu *et al.* 2007). Optimal foraging theory states that birds adopt specific behavioral strategies under different environmental conditions and alter their daily movement patterns and time budgets to meet energy demands and improve energy intake efficiency (Merke and Mosbech 2008; Pecor and Wund 2015). The behavioral activities of Black-necked and Common cranes were influenced by circadian rhythm when wintering in Caohai Wetland, namely by the time of sunrise and sunset.

Foraging was the most common activity of both species, reflecting the importance of satisfying energy demands for both species during overwintering in Caohai Wetland. Vigilance behavior was more frequent in Common Cranes than in Black-necked Cranes. Previous studies have shown that Common Cranes may cease foraging or even leave foraging sites when subjected to strong interference, leading to discontinuous foraging (Kong *et al.* 2018). Common Cranes are sensitive to human disturbance and may choose to leave areas affected by humans and thus may require more foraging time. In contrast, Black-necked Cranes have higher tolerance to human activities, which allows them easier access to abundant food resources of cultivated land.

We suggest that the Caohai National Nature Reserve should improve wetland conservation, particularly of the shallow water and swamps in the boundary region, which are suitable for roosting Black-necked and Common cranes. In addition, the surrounding cultivated lands should be managed to ensure that abundant food sources are available. Human activities and tourism around the Caohai Wetland should be managed to reduce the effects of human interference on Black-necked and Common Cranes.

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