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Sequential vigilance is unpredictable in reproductive Black-necked Cranes

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Abstract

Background: Vigilance refers to the behavior of animals scanning their surroundings with a main purpose of anti-predation. Whether vigilance can serve the function of anti-predation depends on its unpredictability, meaning instantaneous randomness, sequential randomness, and independence, the three assumptions from Pulliam model (J Theor Biol 38:419, 1973). Here we tested two of these three assumptions in reproductive Black-necked Cranes (*Grus nigricollis*) in Tibetan Plateau: instantaneous randomness and sequential randomness.

Methods: Observations were carried out in July and September of 2014, July and August in 2017 in Selincuo National Nature Reserve, Tibet, with the help of focal sampling method. For instantaneous randomness, we used Kolmogorov–Smirnov test for its negative exponential distribution; for sequential randomness, we used Run test, correlation analysis, and generalized linear model to see if an inter-scan and its previous scan were correlated.

Results: Not similar to some recent studies, we did not find a significant predictable vigilance in this crane. Most inter-scan intervals (86/100, 86.0%) passed negative exponential distribution test, meaning vigilance sequences with instantaneous randomness; most inter-scan intervals (91/100, 91.0%) passed sequential random test, showing vigilance sequences were random organized.

Conclusion: Our results suggest that keeping a vigilance pattern with unpredictability is beneficial to the survival of the Black-necked Cranes, which are facing with both cruel natural environments and high predation risks.

Keywords: Black-necked Cranes, Instantaneous randomness, Sequential randomness

Background

Animals frequently stop feeding and turn to vigilance status, scanning their surroundings. The primary purpose of this behavior is to detect potential predators (Beauchamp 2014, 2015). If the vigilance has a certain pattern or regularity, or called predictability, it will be known and grasped by a potential predator. Based on this information, the observant predator can make attack adjustments to the predictable vigilance. Therefore, the unpredictability of vigilance has become the baseline for animal individuals to survive from predators.

The Pulliam's vigilance model (Pulliam 1973) was proposed based on three assumptions: instantaneous randomness in scan initiation, sequential randomness in the duration of successive inter-scans, and independent scanning by different group members. Instantaneous randomness and sequential randomness both derive from the assumption that scanning is controlled by a single parameter: the rate of scan initiation (Pulliam 1973; Bednekoff and Lima 1998). Instantaneous randomness means that an individual has the same probability of lifting its head during each instant when its head is down, regardless of how long its head has been down already. An individual scanning in such a manner would produce inter-scan intervals following a negative exponential distribution. Such a distribution has no central tendency or 'hump' but, instead, shows a smoothly decreasing slope as longer intervals become geometrically less likely.

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Sequential randomness across scans means that scanning process has no 'memory', and the duration of one scan is not influenced by the duration of the previous scan or inter-scan. If a scan depends on its previous scan or inter-scan, the vigilance pattern would become predictable and can be grasped by predators. Sequential randomness or unpredictability can avoid providing observant predators with useful information about when to launch an attack, because there is no predictability in either the initiation of scans or the duration of successive inter-scans (Bednekoff and Lima 1998). In fact, whether the vigilance behavior can be predictable or not has been controversial for a long time. The instantaneous randomness has been found in some studies (Bertram 1980), but still not in others (Lendrem et al. 1986; Beauchamp 2006). The sequential randomness, was similarly supported in some species (Roberts 1994; Suter and Forrest 1994; Li et al. 2017), but not in others (Ferrière et al. 1999; Beauchamp 2006; Pays et al. 2010; Carro et al. 2011).

In this study, we want to test the instantaneous randomness and sequential randomness in reproductive Black-necked Cranes (*Grus nigricollis*), a big bird living only on plateau (Li and Li 2005). As for the third assumption, we shall discuss in our further works and will not mention in this article. A recent report on these cranes has found that the sequential vigilance was unpredictable when they are wintering in Linzhi County, Tibet (Li et al. 2017). But it remains a question that whether they keep their vigilance unpredictable when they migrate up to a breeding area with higher altitude? Our focal population resides in an extremely cruel habitat, with an elevation of about 4700 m asl, strong wind, solar radiation, and very limited food resources. Due to its large size, the crane was formerly considered to have few natural enemies, especially for adults (Li and Li 2005). Nevertheless, Feral Dogs (*Canis familiaris*) have been increasing dramatically in recent decades, and have become a big threat to the cranes (Farrington and Zhang 2013; Kumar and Paliwal 2015). Other predators, including Golden Eagle (*Aquila chrysaetos*) and Eurasian Lynx (*Lynx lynx*), are also potential predators in the area. Human disturbance, especially grazing activities, might also affect vigilance of the cranes (Bishop et al. 1998; Bishop and Li 2002; Yang et al. 2016a, b; Che et al. 2018). Therefore, we predict that the reproductive cranes should scan randomly thus to reduce the possibility of being grasped of their vigilance information and therefore being attacked from predators. Two predictions were made according to the two assumptions: (1) a random pattern of inter-scan intervals, thus making a negative exponential distribution; (2) an unrelated relationship between an inter-scan and its previous scan, thus making a random vigilance sequence.

Methods

Area and species

Observations were carried out in July and September of 2014, July and August of 2017 in Selincuo National Nature Reserve, Tibet, China (30°59′39.79″N, 89°06′49.98″E). The reserve was established in 1993 for protecting rare Tibetan wildlife, including Black-necked Cranes, Snow Leopards (*Panthera uncia*), Tibetan Antelopes (*Pantholops hodgsonii*). The area is about 1640 km^2, with an average elevation of more than 4700 m asl. The reserve is dominated by the semi-arid monsoon climate with thin air, strong solar radiation, cold and dry climate. The mean temperature is about 8 °C in summer, but the temperature difference is large. Sometimes it can rise up to more than 20 °C at noon, and then drops to 0 °C at night. Summer can be called wet or rainy season since more than 80% of the total annual precipitation falls in summer. The reserve area is primarily alpine meadows dominated by *Sophora moorcroftiana*, *Ceratostigma minus*, *Aristida triseta*, *Orinus thoroldii*, *Pennisetum centrasiaticum*, and *Stipa purpurea*.

Black-necked Cranes have a global population of about 6600 individuals (Yang et al. 2016a, b). Qinghai-Tibet Plateau is their main breeding area, while the wintering areas are mainly in south-central Tibet, the Yunnan-Guizhou Plateau in southwest China, India and Bhutan (Qian et al. 2009; Farrington and Zhang 2013; Khan et al. 2014). Black-necked Cranes migrate from wintering areas to the central part of the Selincuo Nature Reserve in early April, breed and live in the reserve until October. Summer cranes have two social units: family groups and social groups. Family groups consist of two adult cranes and one or two nestlings, while social groups are made up of several juveniles.

Behavioral observations

Every day we drove from a little town Maiba, where we stayed, heading to one of three directions: Xiongmei, Bange, or Shenza, to find the cranes from 9:00 to 18:00. In the process, we recorded every Black-necked Crane that we encountered with focal observation method. After locating the Black-necked Cranes with binoculars (Nikula 8 × 42), a video camera (Nikon D7100) was used for recording. Each group or individual was recorded for about 20 min. We used tripods throughout the recording process to stabilize the cameras. We stopped recording if any visual disturbances occurred, such as passing human vehicles or large grazing herds. During the reproductive season, the cranes are loyal to their territories (Li and Li 2005). So we recorded the GPS information of each family or individual, thus to avoid resampling same individual on a same day (they all have their own certain territory during reproductive season, especially for those

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Table 1 Goodness-of-fit of inter-scan intervals of reproductive Black-necked Cranes for negative exponential distribution test

ID	n	λ	p	ID	n	λ	p
1A	28	− 0.118	0.204	28A	22	− 0.189	0.280
2A	*31*	–	*0.024*	29A	39	− 0.323	0.274
3A	*54*	–	*0.001*	30A	54	− 0.302	0.104
3B	30	− 0.100	0.508	*31A*	*20*	–	*0.034*
4A	36	− 0.147	0.367	31B	28	− 0.190	0.358
5A	26	− 0.109	0.980	31C	31	− 0.359	0.455
6A	19	− 0.086	0.993	31D	41	− 0.238	0.580
7A	19	− 0.049	0.163	31E	30	− 0.112	0.751
7B	24	− 0.154	0.853	*31F*	*51*	–	*0.005*
7C	19	− 0.079	0.616	32A	20	− 0.578	0.065
7D	28	− 0.239	0.921	32B	30	− 0.719	0.334
7E	29	− 0.216	0.341	33A	25	− 1.153	0.076
7F	22	− 0.275	0.758	34A	26	− 1.044	0.862
7G	25	− 0.440	0.583	35A	22	− 0.233	0.100
7H	19	− 0.336	0.870	35B	20	− 0.298	0.985
8A	38	− 0.303	0.214	36A	22	− 0.815	0.967
8B	51	− 0.214	0.140	36B	27	− 1.472	0.059
9A	27	− 0.089	0.232	37A	22	− 0.879	0.502
9B	34	− 0.250	0.745	38A	38	− 1.354	0.098
10A	26	− 0.083	0.125	38B	41	− 1.155	0.284
11A	41	− 0.164	0.054	39A	43	− 0.248	0.217
12A	*49*	–	*0.033*	39B	25	− 1.568	0.144
12B	32	− 0.188	0.324	40A	27	− 0.455	0.428
13A	31	− 0.415	0.270	41A	87	− 0.186	0.257
14A	*52*	–	*0.002*	*41B*	*84*	–	*0.024*
15A	52	− 0.521	0.125	42A	40	− 0.443	0.524
16A	43	− 0.356	0.386	42B	58	− 0.303	0.227
16B	*95*	–	*0.004*	43A	32	− 0.276	0.180
17A	*80*	–	*0.001*	44A	54	− 0.238	0.653
17B	108	− 0.387	0.091	44B	48	− 0.181	0.333
18A	23	− 0.538	0.762	45A	23	− 0.266	0.736
19A	30	− 0.216	0.517	45B	36	− 0.390	0.573
19B	28	− 0.216	0.617	46A	33	− 0.502	0.157
19C	*43*	–	*0.003*	46B	42	− 1.241	0.106
19D	28	− 0.185	0.478	47A	26	− 0.959	0.797
19E	33	− 0.328	0.889	48A	22	− 0.233	0.100
19F	27	− 0.111	0.329	48B	20	− 0.484	0.949
20A	20	− 0.191	0.474	49A	23	− 0.830	0.728
21A	23	− 0.381	0.398	49B	27	− 1.472	0.059
21B	*50*	–	*0.046*	49C	26	− 0.693	0.370
22A	*72*	–	*0.016*	50A	22	− 0.879	0.502
22B	48	− 0.198	0.436	*51A*	*38*	–	*0.044*
23A	60	− 0.243	0.470	51B	41	− 1.155	0.284
23B	47	− 0.181	0.838	52A	42	− 0.242	0.157
24A	39	− 0.138	0.311	52B	24	− 1.546	0.174
24B	55	− 0.148	0.834	53A	29	− 0.195	0.298
25A	40	− 0.837	0.098	54A	20	− 0.146	0.454
25B	*33*	–	*0.021*	54B	26	− 0.101	0.140
26A	26	− 1.522	0.055	55A	26	− 0.080	0.347
27A	28	− 0.992	0.154	55B	21	− 0.366	0.519

Significant cases were in italics. While numbers represent the group number and the letters represent the individuals from the same group

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families that carry nestlings and were about to have nestlings, so it is basically impossible that one same family was sampled on more than one occasion). Weather, day time, group type and group size were also recorded at the same time. Observations were only made on sunny or cloudy days thus to avoid potential effect of bad weathers.

Data analysis

A focal observation includes a sequence of scans and inter-scans. We totally collected 208 focal samples with a total time of about 2400 min. Samples less than 10 min, or with less than 20 feeding/vigilance transitions, or with visible disturbances were deleted, and thus 100 samples from 55 groups were left. We reviewed all these samples and timed scans and inter-scans to the nearest 1 s.

For instantaneous randomness, we used Kolmogorov–Smirnov test to examine the distribution of inter-scans of each vigilance sequence. We considered the inter-scan intervals were randomly organized if they passed the negative exponential distribution test, and then we calculated its parameter λ, which was the only determinant of the distribution.

Since most sequences of our samples included less than 30 transitions, we tested sequential randomness of inter-scan intervals with nonparametric one-sample runs test (Beauchamp 2006). Median value was set as the cut point. This test was used to assess whether long (>median value) or short (<median value) inter-scans occurred together in the sequence more often than expected by chance. Rejection of random test provides evidence for a nonrandom pattern of vigilance sequence. We also used a generalized linear model to assess whether every inter-scan interval was dependent on the previous scan duration (Pays et al. 2010). The previous scan duration was set as an independent variable. Family or group ID was set as a random factor. For each independent sample, we also used Pearson correlation when data were normally distributed or Spearman rank correlation when data were not normally distributed to evaluate whether the inter-scan intervals and the previous scan durations were closely related (Li et al. 2017).

All statistical analyses were carried out with SPSS (version 20.0). The level of statistical significance was set at $p = 0.05$, and data were reported as mean ± SE.

Results

We totally included 100 vigilance sequences in our database; the average duration of inter-scan intervals was 20.3 ± 0.4 s, ranging from 1 to 331 s, whereas the average scan duration was 6.6 ± 0.3 s, ranging from 1 to 215 s. For the instantaneous randomness, 86 sequences passed Kolmogorov–Smirnov test for the negative exponential distribution, meaning that 86.0% sequences interrupted

feeding and scanned their surroundings randomly. The parameters of each negative exponential function were shown in Table 1, and the grouped inter-scan intervals were shown as Fig. 1.

For the sequential randomness, runs tests revealed that most sequences of inter-scan intervals (91/100, 91.0%) could be considered as non-significant correlation or random organized, and only 9 sequences were in nonrandom order (Table 2). The correlation analysis between the previous scan and the current inter-scan also showed an unpredictable correlation in most cases (92/100, 92.0%). Only 8 sequences showed a negative or positive correlation (Table 2). From the generalized linear model, there was no significant correlation between the previous scan and the current inter-scan ($F_{1, 3489} = 3.212$, $p = 0.0732$), although the group ID had a significant effect on inter-scan intervals ($F_{99, 3489} = 4.939$, $p < 0.001$).

Discussion

The randomness or unpredictability is probably the baseline of whether vigilance can serve its main function of anti-predation. We tested the two main assumptions of the classical group-size-effect model proposed by Pulliam in 1973, namely the instantaneous randomness and the sequential randomness. Our results showed that most of the inter-scan intervals of the Black-necked Cranes can be considered as randomly organized.

Instantaneous or sequential randomness of vigilance did not receive supports from most recent studies (Beauchamp 2006; Pays et al. 2010; Carro et al. 2011), but it did from some other studies (Bertram 1980; Li et al. 2017), just like what we found in this study of reproductive Black-necked Cranes. Actually, using a random or regulative strategy for a vigilant animal is probably depending
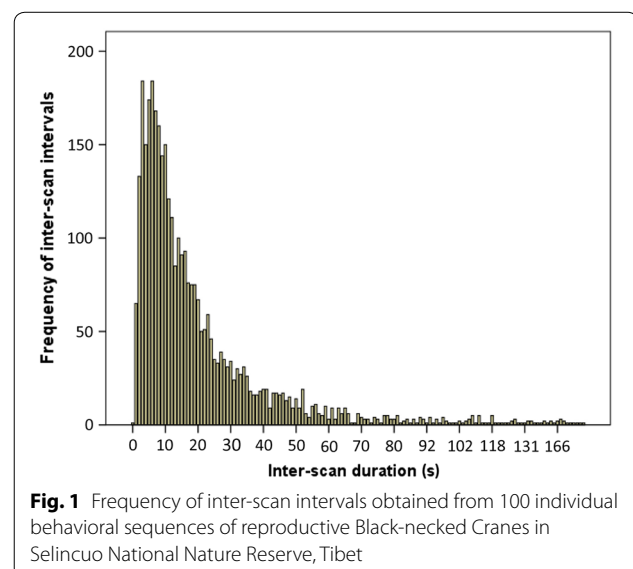

Fig. 1 Frequency of inter-scan intervals obtained from 100 individual behavioral sequences of reproductive Black-necked Cranes in Selincuo National Nature Reserve, Tibet

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Table 2 Run test and correlation test of inter-scan intervals and scan durations in reproductive Black-necked Cranes in Tibet

ID	n	Run		Correlation		ID	n	Run		Correlation	
		Z	p	r	p			Z	p	r	p
1A	28	− 0.940	0.347	0.153	0.437	28A	22	− 0.655	0.512	0.251	0.260
2A	31	− 1.457	0.145	0.239	0.196	29A	39	− 0.289	0.773	0.071	0.669
3A	54	− 0.550	0.583	− 0.034	0.808	30A	54	− 1.239	0.215	− 0.037	0.792
3B	*30*	*− 1.301*	*0.193*	*− 0.383*	*0.037*	31A	20	0.689	0.491	0.371	0.107
4A	*36*	*− 2.198*	*0.028*	0.131	0.447	31B	28	0.000	1.000	− 0.047	0.811
5A	26	− 0.976	0.329	− 0.272	0.179	31C	31	− 1.726	0.084	− 0.063	0.736
6A	19	− 0.935	0.350	− 0.252	0.298	31D	41	− 0.313	0.755	0.060	0.709
7A	19	0.486	0.627	0.411	0.080	31E	30	0.186	0.853	− 0.243	0.196
7B	24	− 0.626	0.531	0.139	0.516	31F	51	− 1.253	0.210	− 0.188	0.186
7C	19	0.012	0.990	0.324	0.176	32A	20	0.279	0.781	− 0.180	0.447
7D	28	− 0.553	0.580	− 0.232	0.235	32B	30	− 0.929	0.353	− 0.200	0.289
7E	29	0.000	1.000	− 0.261	0.171	*33A*	*25*	*− 2.000*	*0.046*	0.340	0.097
7F	*22*	*− 1.529*	*0.126*	*− 0.548*	*0.008*	*34A*	*26*	*− 3.403*	*0.001*	0.013	0.948
7G	25	− 0.810	0.418	− 0.183	0.381	35A	22	− 1.092	0.275	0.102	0.653
7H	19	0.486	0.627	− 0.211	0.387	35B	20	− 0.689	0.491	0.226	0.337
8A	38	0.000	1.000	0.140	0.400	36A	22	− 1.503	0.133	− 0.186	0.408
8B	51	0.860	0.390	0.097	0.498	36B	27	0.793	0.428	− 0.035	0.864
9A	27	− 0.779	0.436	0.202	0.311	37A	22	1.583	0.113	0.200	0.372
9B	34	− 0.174	0.862	0.018	0.918	38A	38	− 1.480	0.139	− 0.022	0.895
10A	26	− 1.001	0.317	− 0.197	0.334	38B	41	1.499	0.134	− 0.151	0.345
11A	*41*	*1.270*	*0.204*	*− 0.331*	*0.034*	*39A*	*43*	*− 1.850*	*0.064*	*− 0.381*	*0.012*
12A	49	− 0.509	0.611	− 0.075	0.608	39B	25	− 0.340	0.734	− 0.019	0.927
12B	*32*	*− 0.898*	*0.369*	*− 0.361*	*0.042*	40A	27	− 0.779	0.436	0.151	0.452
13A	31	− 0.726	0.468	0.058	0.755	41A	87	− 1.617	0.106	− 0.124	0.253
14A	*52*	*− 1.961*	*0.050*	*− 0.057*	*0.688*	41B	82	− 0.439	0.660	− 0.169	0.130
15A	*52*	*0.011*	*0.991*	*0.300*	*0.031*	42A	40	− 1.762	0.078	− 0.161	0.320
16A	43	− 1.232	0.218	− 0.066	0.673	42B	58	− 0.762	0.446	0.091	0.499
16B	*95*	*− 3.346*	*0.001*	0.110	0.288	43A	32	− 0.539	0.590	− 0.048	0.794
17A	80	− 1.500	0.134	− 0.037	0.747	44A	54	− 0.815	0.415	0.036	0.795
17B	108	− 1.094	0.274	− 0.148	0.126	44B	48	− 0.134	0.893	− 0.182	0.215
18A	*23*	*− 0.846*	*0.398*	*− 0.654*	*0.001*	45A	23	0.000	1.000	− 0.296	0.170
19A	30	0.212	0.832	0.152	0.422	*45B*	*36*	*− 2.536*	*0.011*	− 0.311	0.069
19B	28	− 0.193	0.847	− 0.110	0.576	46A	33	0.713	0.476	− 0.076	0.676
19C	43	− 0.305	0.760	− 0.039	0.805	46B	42	− 1.299	0.194	0.075	0.636
19D	28	1.383	0.167	− 0.064	0.745	*47A*	*26*	*− 3.002*	*0.003*	− 0.242	0.233
19E	33	− 0.225	0.822	0.022	0.904	48A	22	− 1.092	0.275	0.102	0.653
19F	27	1.580	0.114	− 0.285	0.150	48B	20	− 0.689	0.491	0.035	0.883
20A	20	− 0.230	0.818	0.060	0.801	49A	23	− 1.653	0.098	− 0.270	0.212
21A	23	− 0.846	0.398	− 0.094	0.670	49B	27	0.793	0.428	− 0.035	0.864
21B	50	− 1.429	0.153	− 0.269	0.059	49C	26	− 0.573	0.566	0.206	0.314
22A	70	− 0.963	0.335	− 0.216	0.072	50A	22	1.583	0.113	0.122	0.589
22B	48	0.146	0.884	0.039	0.791	51A	38	− 1.480	0.139	− 0.046	0.782
23A	*60*	*− 2.604*	*0.009*	0.205	0.116	51B	41	1.499	0.134	− 0.151	0.345
23B	47	0.003	0.997	− 0.109	0.464	*52A*	*42*	*− 1.718*	*0.086*	*− 0.346*	*0.025*
24A	39	− 0.970	0.332	− 0.044	0.788	52B	24	− 0.175	0.861	− 0.009	0.966
24B	*55*	*− 2.312*	*0.021*	0.014	0.917	53A	29	0.007	0.995	− 0.345	0.067
25A	40	− 1.442	0.149	− 0.223	0.167	54A	20	− 0.230	0.818	− 0.147	0.536
25B	33	− 0.349	0.727	− 0.144	0.423	54B	26	− 0.600	0.548	0.012	0.955
26A	26	− 0.170	0.865	− 0.047	0.821	55A	26	− 0.976	0.329	0.054	0.793
27A	28	− 0.871	0.384	0.116	0.558	55B	21	0.011	0.991	− 0.039	0.868

Significant cases were in italics. While numbers represent the group number and the letters represent the individuals from the same group

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on their environmental surroundings, especially the predation risk. If feeding is too risky, especially with stalking predators present, animals will make themselves unpredictable; otherwise detection of predation risk should be achieved better by regular scanning. In former studies that rejected vigilance randomness, there were no natural enemies for Greater Flamingos (*Phoenicopterus ruber ruber*) (Beauchamp 2006) and Greater Rheas (*Rhea Americana*) (Carro et al. 2011) in South America. These large birds are sensitive to human disturbance (Galicia and Baldassarre 1997; Baldassarre and Arengo 2000; Yosef 2000); however, human disturbance is not like a stalking predation threat in an open landscape of water or grassland. In this case, regular scanning for human disturbance would be a better option and therefore about half of their vigilance sequences can be predicted.

Comparably, although Black-necked Crane is also a large bird, its surviving environments are extremely cruel. The cranes mostly form a family group with only two members during the reproductive season, thus leading to a much smaller group than Greater Flamingos or Greater Rheas. They not only need to survive from high altitude, low temperature, thin air and starvation, and take care of their offspring, but also need to face threatens from human or stalking predators such as Eurasian Lynx. And even non-stalking predators such as stray dogs could adopt a stalking strategy to catch local birds (Li et al. 2017; Yang et al. 2019). Therefore, keeping vigilance unpredictable was very essential for the survival of these rare Black-necked Cranes.

Conclusion

Similar to our previous findings during winter period (Li et al. 2017; Che et al. 2018), Black-necked Cranes also kept their vigilance unpredictable during the breeding season, meaning that both instantaneous randomness and sequential randomness were supported. Keeping a vigilance pattern with randomness or unpredictability is beneficial to the survival and reproduction of the Black-necked Cranes, which are facing with both cruel natural environments and high predation risks.

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