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Short report

Can sequential vigilance be predicted?

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ABSTRACT

Sequential randomness is one of the three important assumptions for Pulliam's vigilance model (1973). Here we tested the sequential randomness in Black-necked cranes *Grus nigricollis*, to see if the vigilance sequence can be predicted. Not similar to other recent studies, we found that most vigilance sequences (44/46) passed runs randomness test, and the length of an inter-scan interval was usually unrelated to its previous scan duration. Our findings suggest high predation risk might favor a random pattern of vigilance.

1. Introduction

Animals frequently interrupt feeding, and raise their heads to look around their surroundings. This behavior, vigilance, serves mostly as a detection of potential predators (Beauchamp, 2014; Beauchamp, 2015). The effects of vigilance strategies were firstly theorized by Pulliam, (1973), and this model was based on three assumptions, independent scanning by group members, instantaneous randomness in scan initiation, and sequential randomness across scans (Pulliam, 1973; Bednekoff and Lima, 1998).

Studies that tested whether animals scan independently have obtained opposite results. Independent scanning have been observed in ostriches *Struthio camelus* (Bertram, 1980), but not in many other species (e.g. (Lendrem et al., 1986; Beauchamp, 2006; Carro and Fernandez, 2009). Recent studies indeed revealed that animals actually react to their group members, thus leading to a coordinated vigilance pattern, like in common cranes *Grus grus* (Ge et al., 2011), or a synchronized vigilance pattern (Pays et al., 2007; Beauchamp et al., 2012), like in red-necked pademelon *Thylogale thetis* (Pays et al., 2009). The second rule, instantaneous randomness means that an individual has the same probability of raising its head during each instant when its head is down, regardless of how long its head has been down already, and thus resulting in a negative exponential distribution of inter-scan intervals (Pulliam, 1973; Bednekoff and Lima, 1998). Instantaneous randomness has found in some species (Bertram, 1980; Caraco, 1982), but not in many others (Lendrem et al., 1986; Beauchamp, 2006).

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 (Bednekoff and Lima, 1998). Sequential randomness or unpredictability can avoid providing 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 (Beauchamp, 2006). Two predictions can be made by the rule of sequential randomness, one is the sequence of inter-scan intervals is randomly distributed, and the other is the length of an inter-scan interval is unrelated to the previous scan (Bednekoff and Lima, 1998; Carro et al., 2011). Similarly, support for the sequential randomness is controversial, as some studies reported the presence of sequential randomness (Roberts 1994; Suter and Forrest, 1994), while others described the occurrence of predictability (Ferriere et al., 1999; Beauchamp, 2006; Pays et al., 2010; Carro et al., 2011).

In this study, we want to test sequential randomness of vigilance in Black-necked crane *Grus nigricollis*, a big bird living only on plateau. Because of its large size, the crane was considered to have few natural enemies, especially for adults (Li and Li, 2005). Nevertheless, feral dogs *Canis familiaris* have being increased dramatically in recent decades, and have become a big threat to the cranes (Farrington and Zhang, 2013; Kumar and Paliwal, 2015). Feral dogs are not a traditional stalking predator, but they have been observed several times to adopt a stalking strategy to catch local birds, including Oriental Turtle dove *Streptopelia orientalis* and Tibetan Partridge *Perdix hodgsoniae* (personal observation). Other predators, including golden eagle *Aquila chrysaetos* and desert cat *Felis bieti*, are also potential predators in the wintering area of the cranes (Liu, 2002). Human disturbance, especially agricultural activities, might also affect vigilance of the cranes (Bishop et al., 1998; Bishop and Li, 2002; Li and Li, 2005; Che et al., 2018). Therefore, we predict that adult cranes should scan randomly thus to reduce the possibility of being grasped of their vigilance information and therefore being attacked from predators. Two predictions are as

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following, 1) a random pattern of inter-scan intervals, and 2) an unrelated relationship between an inter-scan and its previous scan.

2. Methods

2.1. Study area

This study was conducted in Yarlung Zangbo Nature Reserve (28° 40′ to 30° 17′ N, 87° 34′ to 91° 54′ E) on Qinghai-Tibet Plateau, China. The Reserve was established in 2002 for protecting the largest wintering population of Black-necked Cranes as well as the alpine wetland ecosystem on which they depend. The Reserve ranges from 3500 m to 4500 m in elevation and encompasses about 6140 km^2. The Reserve is dominated by a semi-arid monsoon climate, but experiences occasional snowfall in winter. The mean temperature in January is −4.7 °C, but ranges from −14.0 °C to 8.0 °C. The Reserve area is primarily alpine meadows dominated by *Sophora moorcroftiana*, *Ceratostigmn minus*, *Aristida triseta*, *Orinus thoroldii*, *Pennisetum centrasiaticum*, and *Stipa purpurea*. Black-necked Cranes mainly use three habitat types in the Reserve: waterside, meadows, and farmland (Bishop et al., 1998; Bishop and Li, 2002).

2.2. Study species

Black-necked Cranes (hereafter, cranes) have a global population of about 6600 individuals (Farrington and Zhang, 2013; BirdLife-International, 2017). Their primary breeding area is the Qinghai-Tibet Plateau and its adjacent regions, 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 breeding areas to the central part of the Yarlung Zangbo Nature Reserve in early December and overwinter in the Reserve until early April (Cangjue et al., 2007; Qian et al., 2009). Wintering cranes have two social units: family groups and social groups. Family groups consist of two adult cranes, with or without one or two juveniles, while social groups are made up of several juveniles or combined family groups (Li and Li, 2005).

2.3. Behavioral observations

Cranes were located during regular route surveys (Kazi route, Hutougou route, Qiangga route, Chundui route) and locations were recorded with a GPS. The route was not repeated on the same day to avoid duplicate sampling. Observations were not made on days with snow or strong winds to lessen any bias caused by the effect of extreme weather.

We used a video camera to record vigilance behavior of Black-necked cranes from December 2015 to January 2016. For each observation, we recorded date, time, location, habitat type (mostly farmland), age (adult or juvenile) and group type (family group, social group). We also assigned each group an independent identification number. To avoid possible effects of group size and age (Li et al., 2013; Xu et al., 2013; Kuang et al., 2014; Yang et al., 2016), we only focused on adult cranes from family groups.

"Vigilance" behavior was defined as a crane stretching its head upward while scanning around. Thus a focal observation included a sequence of scans and inter-scans. Inter-scan behaviors included feeding, walking, preening and other behaviors. Feeding and vigilance accounted for about 80–90% of the time budget during wintering periods (Cangjue et al., 2007; Yang et al., 2016; Che et al., 2018).

2.4. Data analysis

We totally collected 63 family groups with a total time of 1600 min. Samples less than 10 min, or with less than 10 feeding/vigilance transitions, or with visible disturbances were deleted, and thus 46 samples from 27 families were left. We reviewed all these samples and timed scans and inter-scans to the nearest 1 s.

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 firstly used a generalized linear model to assess whether every inter-scan interval was dependent on the previous scan duration (Pays et al., 2010). Dependent inter-scan intervals were lg10 transformed to achieve normality ($P = 0.222$ after transformation). The previous scan duration was set as an independent variable. Since all samples were collected from family groups ranged only from 2 to 4 individuals, group size or called family size was not included in the model. Usually one or at most two adult individuals were focally sampled from each family, thus family 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 closed related. All statistical analyses were carried out with SPSS (version 19.0). The level of statistical significance was set at $P = 0.05$, and data were reported as mean ± SE.

3. Results

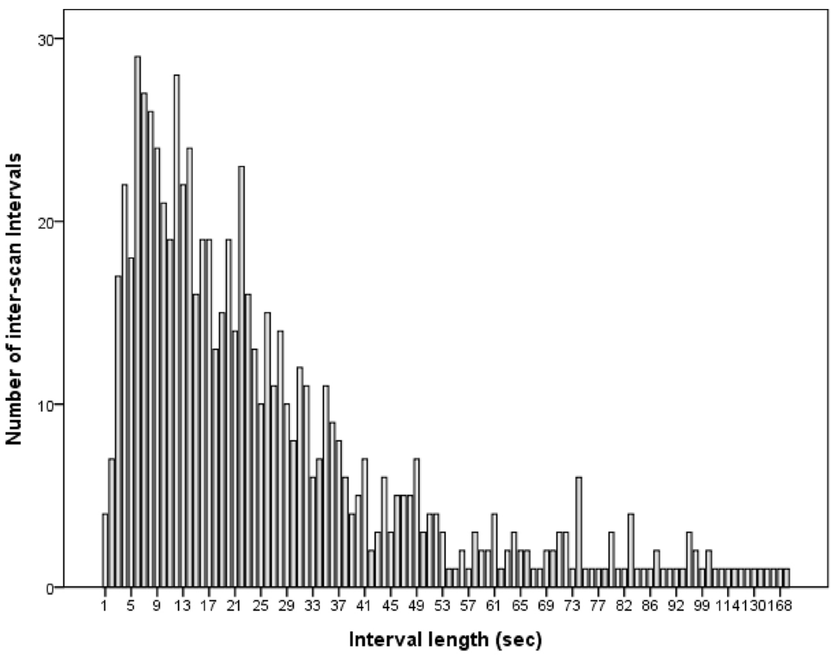
The length of inter-scan intervals varied from 1 to 192 s, with a median of 20 s (Fig. 1A), whereas the scan durations varied from 1 to 128 s, with a median of 4 s (Fig. 1B). Runs tests revealed that most sequences of inter-scan intervals (44/46, 95.7%) could be considered as random organized or unpredictable, and only 2 sequences (ID: A31 & A37, 4.3%) were in nonrandom order (Table 1). Examples of a random and nonrandom sequence were shown in Fig. 2.

Within the generalized linear model, family ID had a significant effect on the inter-scan duration ($F_{26,672} = 5.186$, $P < 0.001$). However, no significant relationship was found between the previous scan and the current inter-scan ($F_{1,672} = 0.713$, $P = 0.399$). According to the correlation analysis, most individuals (44/46, 95.7%) showed an unpredictable correlation, and only 2 individuals (ID: A13 & B40) showed a positive correlation (Table 1). Examples of a predictable and unpredictable vigilance sequence were shown in Fig. 3.

4. Discussion

We tested the hypothesis that vigilance sequences of Black-necked cranes were randomly distributed assumed by Pulliam's model (1973). For the sequence of inter-scan intervals, 44 out of 46 samples passed the random test, indicating that the cranes interrupt feeding to scan their surroundings randomly. Similarly, 44 out of 46 samples showed an unrelated correlation between a scan and its subsequent inter-scan, revealing an unpredictability of an inter-scan by its previous scan. Both results suggest sequential randomness across scans in Black-necked cranes.

Black-necked cranes were formerly considered as a large water bird with few natural enemies (Bishop and Li, 2002; Li and Li, 2005). However, as an increasing threat for both human and wildlife, the population of feral dogs has dramatically increased in recent decades all over Tibet. These free-roaming dogs usually form a structured group and can use a stalking strategy to predate on Tibetan wildlife, including both Tibetan ungulates and Black-necked cranes (Farrington and Zhang, 2013; Kumar and Paliwal, 2015; Home et al., 2017). A recent report by Shanshui Conservation Center of China showed that feral dogs can attack Black-necked cranes, especially juveniles (Shanshui Conservation Center, 2017). So the wintering cranes have to keep



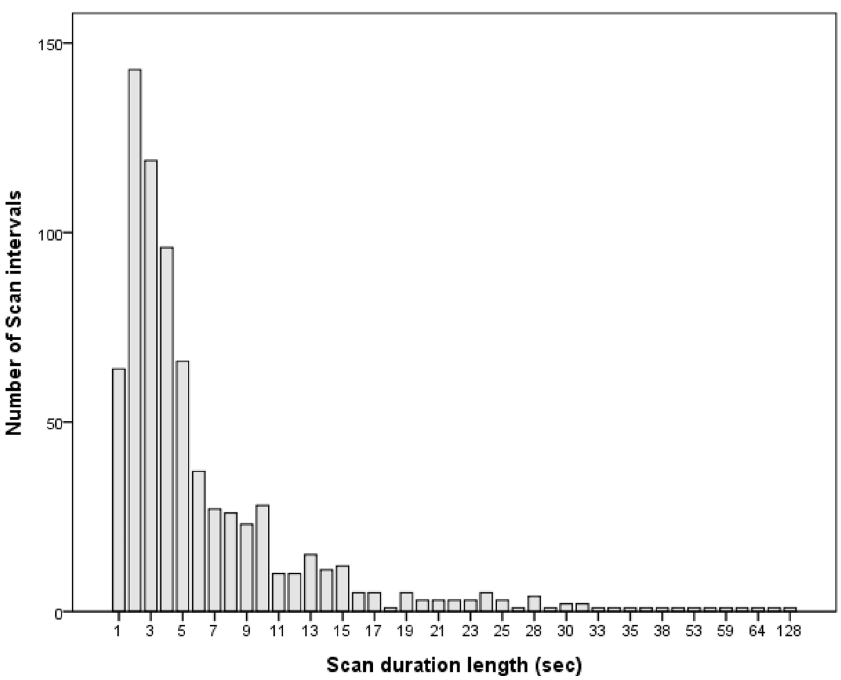


Fig. 1. Frequency of inter-scan intervals (a) and scan duraitons (b) from 46 individuals of wintering Black-necked cranes in Tibet.

vigilant, since most of them feed in farms where feral dogs are common.

Using similar research methods, some recent studies showed a certain predictable pattern of vigilance. In flamingos *Phoenicopterus ruber*, 24 out of 58 sequences departed from randomness, and some inter-scan intervals with similar length even occurred continuously (Beauchamp, 2006). In 40 vigilance sequences of rheas *Rhea americana*, 7 departed from randomness, and 12 showed a positive or negative correlation between an inter-scan interval and its previous scan (Carro et al., 2011). Actually in both above examples, there were no natural enemies except humans, and so the predation risk was extremely low (Beauchamp, 2006; Carro et al., 2011). In this case, detection of human disturbance becomes the main target and it should be achieved best by regular scanning. Upon detection, flamingos or rheas can choose to stay or leave the area, depending on the distance between the source of human disturbance and themselves.

Sequential randomness may be much more efficient under high level of predation risk. Preys should avoid producing a predictable and regular vigilance pattern, thereby reducing the possibility that the predator can launch an attack (Beauchamp, 2006; Carro et al., 2011). Although feral dogs are not stalking predators, they are usually grouped, structured, and can also adopt a stalking strategy (Kumar and Paliwal, 2015; Home et al., 2017). If the cranes adopted a regular strategy, such as a stable sequence with similar inter-scan intervals, or a long scan followed a long inter-scan, there is a possibility that this vigilance information would be collected and used by feral dogs, and the risk of being attacked would be higher. Avoiding predictable behavioral sequences would be an effective anti-predatory strategy.

Table 1
Randomness and correlation test of inter-scan intervals and scan durations in wintering Black-necked cranes in Tibet. "*" indicates significant at 0.05, "#" indicates a non-parametric correlation test (Spearman) between scan interval and consequent inter-scan interval.

ID	N	Runs		Correlation		ID	N	Runs		Correlation	
		Z	P	r	P			Z	P	r	P
A1	17	−0.488	0.626	0.016	0.951	A34#	18	0.729	0.466	−0.264	0.289
B1	15	0.018	0.986	−0.017	0.951	B34#	25	−0.755	0.450	−0.113	0.590
A6	11	0.671	0.502	0.325	0.329	B35	10	−1.006	0.314	−0.584	0.076
B6	10	0.000	1.000	0.254	0.480	A37	17	−2.454	.014*	0.271	0.292
A9	14	0.835	0.404	0.194	0.507	B37	22	−1.529	0.126	0.245	0.272
B9	11	−1.254	0.210	0.115	0.736	A38	20	−0.689	0.491	0.254	0.281
A10	26	−1.401	0.161	−0.127	0.537	B38	21	−0.817	0.414	−0.172	0.457
B10	28	0.309	0.757	0.065	0.743	A40	22	−0.218	0.827	−0.181	0.419
A11	11	0.029	0.977	−0.322	0.334	B40	22	1.092	0.275	0.442	0.039*
B11	16	−0.259	0.796	0.024	0.931	A41#	18	0.243	0.808	0.384	0.115
A13	21	0.098	0.922	0.478	0.028*	B41	17	−0.991	0.322	0.289	0.261
B13	20	0.743	0.457	0.209	0.376	B42	10	0.335	0.737	−0.419	0.228
A14	18	0.729	0.466	−0.227	0.365	A43	12	0.303	0.762	0.003	0.994
B14	14	−0.835	0.404	0.022	0.940	B43#	17	0.000	1.000	0.198	0.447
A19	17	0.015	0.988	−0.061	0.816	A46	14	0.835	0.404	0.067	0.819
B19	16	1.294	0.196	0.247	0.356	A47	10	0.492	0.623	−0.393	0.261
A21	13	−1.144	0.253	−0.044	0.887	A50	15	0.018	0.986	−0.480	0.070
A22	13	−1.144	0.253	0.293	0.331	B50	15	−1.059	0.290	−0.046	0.870
B22#	14	0.000	1.000	0.378	0.182	B51#	24	−0.209	0.835	−0.066	0.758
B25	10	0.335	0.737	0.248	0.490	A52	15	1.095	0.274	−0.142	0.614
A30	13	−1.144	0.253	−0.394	0.183	B52	14	0.000	1.000	−0.017	0.955
B30	18	−1.215	0.224	−0.084	0.747	A60	15	−0.521	0.603	0.325	0.329
A31	13	−2.310	.021*	0.309	0.304	B60	14	−0.835	0.404	0.008	0.977

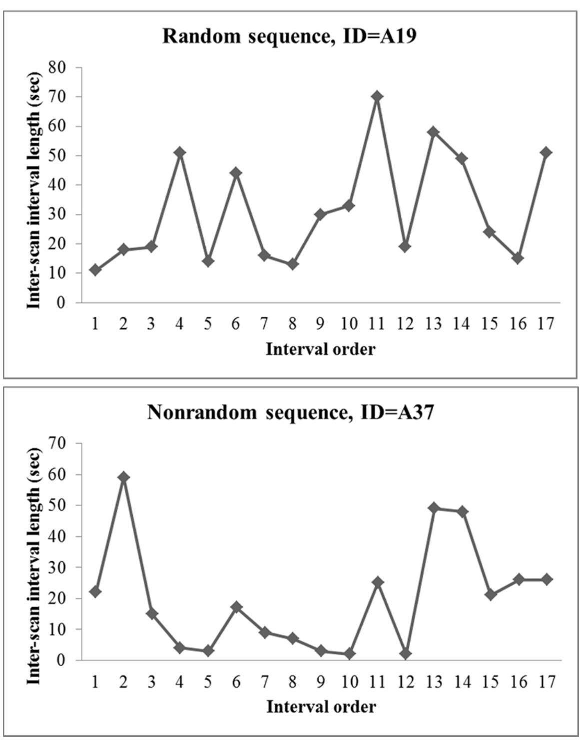


Fig. 2. Examples of random and nonrandom sequence of inter-scan intervals in wintering Black-necked cranes in Tibet.

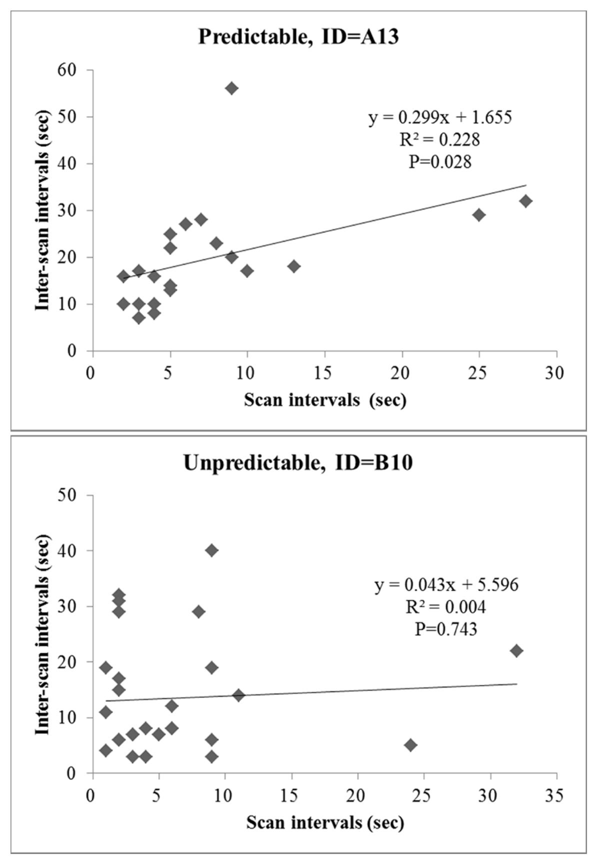


Fig. 3. Examples of predictable and unpredictable correlation between the current inter-scan interval and the previous scan duration in wintering Black-necked cranes in Tibet.

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