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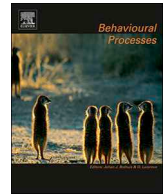
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# Vigilance strategy differentiation between sympatric threatened and common crane species

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## ABSTRACT

Studies have indicated that threatened species may show reduced or elevated antipredator behavior compared with their close common relatives, but remarkably few studies revealed such differences in behavior among populations. Exploring factors affecting behavior between phylogenetically related common and threatened species could help understand such discrepancy. We tested for effects of external and internal variables including month, time of day, habitat type, distribution area, group composition status and group size on vigilance behavior (including group scan frequency and level) of two sympatric common *Grus grus* and threatened *G. nigricollis* cranes with generalized linear models. We detected significant species effect on group scan level, and *grus* was more vigilant than *nigricollis*. Model tests also indicated that group size had common effect on group scan frequency for both species, and distribution area significantly correlated with the vigilance of *nigricollis*, while *grus* was more affected by time of day and group composition status in areas of sympatry with *nigricollis*. But when *nigricollis* was absent, time had no effects on behavior by individuals belonging to *grus*, implying existence of inter-specific competition. We also found that *grus* decreased individual vigilance efforts by foraging with other species (e.g., Bar-headed Goose *Anser indicus*) to share large group alertness benefits (collective vigilance). As our results demonstrated, we argued that, with diverse antipredation tactics e.g., foraging with other species, alternating time rhythm or partitioning spatial utilization to mitigate inter-specific competition, reducing time allocation to preening while maintaining foraging efforts, common *grus* could maintain high level of vigilance, which may benefit their survival and population increase. Whereas less time spent vigilant antipredation strategy adopted by threatened *nigricollis*, this may have negative effects on their populations.

## 1. Introduction

Vigilance refers to the alertness state of animals (for birds, vigilance could usually be distinguished from the head-up posture), severing as a behavioral reaction of animals to detect or monitor putative predators or rivals (Caro, 2005; Beauchamp, 2015); it is also the key component and precondition of anti-predatory or defensive behavior (Dugatkin, 2004; Tyrrell and Fernández-Juricic, 2015).

Animals likely have higher survival prospects when detecting a potential predator earlier and fleeing at a longer distance (Cooper and Blumstein, 2015), but they may suffer from disruption of normal activities by potential predators more frequently, resulting in reduced foraging or reproductive failure and hence population decline (Møller,

2008; Møller et al., 2014). A common cause of threat status is susceptibility to potential predators reporting that threatened bird species show stronger antipredator response (e.g. longer flight initiation distance) compared to closely related common species (Jiang and Møller, 2017a), when great inter-pair variance and sampling difference still existed. However, Jiang and Møller (2017b) found that antipredator behavior is related to genetic variance (band sharing coefficient, heterozygosity and inbreeding coefficient), and made the prediction that with lower genetic variability threatened species have reduced antipredator behavior, and supported by many case studies (Thaxter et al., 2010; Møller et al., 2014). These opposite reports remind us of the complexity of anti-predatory vigilance behavior and highlight species / population specifics (Møller et al., 2014).

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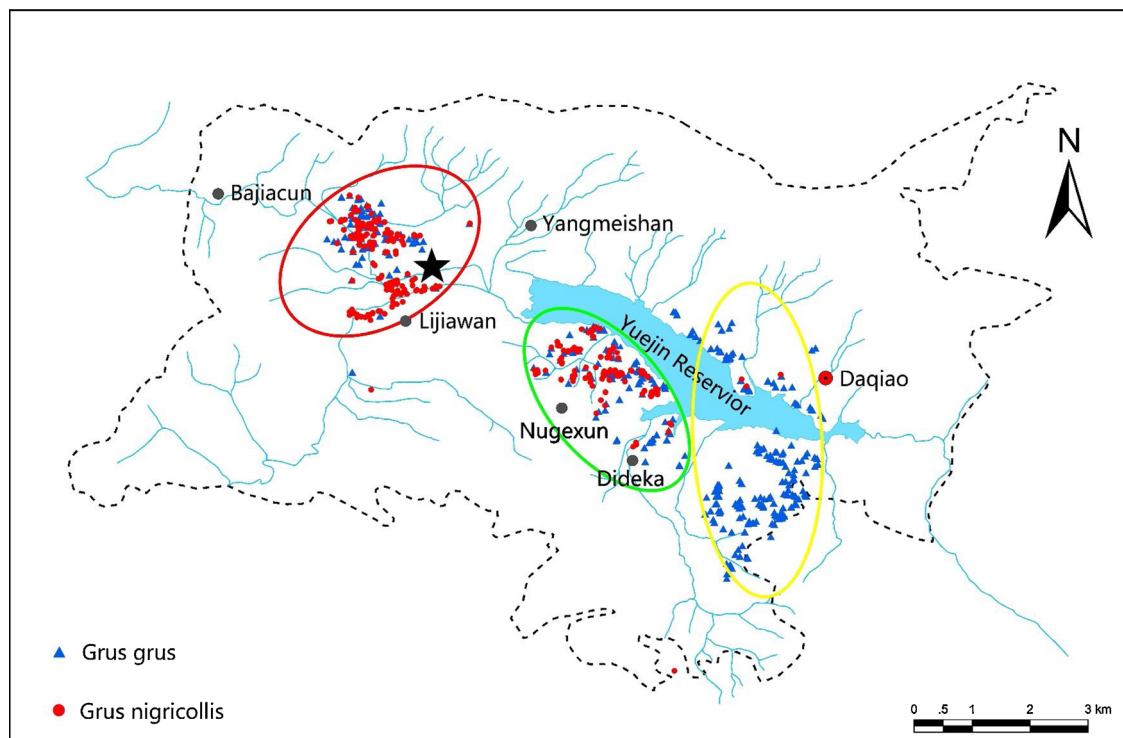
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**Fig. 1.** Spatial distribution of *Grus grus* and *G. nigricollis* in Huize National Nature Reserve, Yunnan, SW China. The black dots indicate administrative villages, and Daqiao is the town capital; blue area and lines show the Yuejin reservoir and rivers; black star indicates the roosting site. The red, green and yellow circles indicate the three relative separated areas of Yangmeishan-Baijiacun-Lijiawan (YBL), Nugexun-Dideka (ND) and Dideka-Daqiao (DD) where *grus* and *nigricollis* co-occurred in the YBL and ND area, and only *grus* was present in the DD area.

Numerous studies on all aspects of vigilance behavior were conducted, especially the inverse interaction between individual vigilance and group size, the well-known “group size effect” (see reviews of Elgar, 1989; Roberts, 1996). By gathering in big flocks, group members seek collective benefits from “many eyes effects” (Pulliam, 1973; Powell, 1974) or reduction in individual risk through “dilution effect” (Bertram, 1978; Pulliam et al., 1982; Lima, 1990). So, flocking as an effective antipredator behavior has been intensively adopted by nonhuman animals (Elgar, 1989; Caro, 2005; Beauchamp, 2015).

While aggregative behavior is commonly observed, many other antipredatory reactions have evolved including camouflage, mobbing and inspection behavior, unpredictable mass or evasive movement, but also flight from putative predators (Dugatkin, 2004). Different behavioral reactions may be selected by different organisms (species or individuals), causing fitness differences and causing corresponding impacts on populations (Thaxter et al., 2010; Møller et al., 2014; Jiang and Møller, 2017a, b).

As external expression of internal responses, animal behavior refers to a series of complex decision-making progresses that are affected by both biological factors including genetic background, learning and cultural transmission (Dugatkin, 2004), but also environmental factors, including season (Xia et al., 2011), habitat type (Kong et al., 2011; Li et al., 2013), disturbance (Wang et al., 2011; Li et al., 2016) and group related factors e.g. classic group size, position in the group, group composition status and group predation vulnerability (see review in Elgar, 1989; Roberts, 1996). A comprehensive understanding of how environmental and group related variables affect vigilance and how animal responses to these factors could help clarify differences in vigilance among species and understand key factors driving divergence.

In this study, we selected the phylogenetically related sympatric species-pair of common Eurasian Crane *Grus grus* and the threatened Black-necked Crane *G. nigricollis* as our study subjects. To understand vigilance strategy differentiation in these species, we compared interspecific differences in (1) vigilance behavior pattern (time budget) and

(2) vigilance behavior progress (variables affecting behavior expression). We predicted that if there are vigilance differences between such pairs of species, additional behavioral tradeoffs (e.g. foraging or others) associated with predation could be detected. If vigilance behavior was driven by distinct factors, we could identify specific vigilance strategy by taking former studies of habitat selection (Kong et al., 2018) and behavioral rhythms (Luo, 2012) into consideration, which is the supposed underlying force driving population trends.

## 2. Materials and methods

### 2.1. Study species and area

*Grus grus* and *G. nigricollis* are co-generic species of the crane family (Krajewski et al., 2010). With a population of c. 500,000, *grus* has a vast distribution across Eurasia and is listed as a Least Concern (LC) species in IUCN Red List, while the Vulnerable (VU) *nigricollis* has a limited range of 1,900–5,000 m above the sea level (asl.) on the Qinghai-Tibet and Yunnan-Guizhou Plateau with a population of c. 10,000 individuals (IUCN, 2019). These species share wintering grounds on the Yunnan-Guizhou Plateau, SW China allowing us to study them in one site at the same time.

This study was conducted in the Daqiao region (N26°38'00"–26°44'24", E103°12'06"–103°22'02") of Huize National Nature Reserve, Yunnan, SW China. Located in the Yunnan-Guizhou Plateau, the reserve ranges from 2,470 to 3,092 m asl., was first established to protect wintering waterfowl and their habitat in 1990, and upgraded to nation-level reserve in 2006 (Qiou and Yang, 2012). There are 65 waterfowl species with over 3,000 individuals, including c. 400 Black-necked Cranes and 300 Eurasian Cranes there each winter (Qiou and Yang, 2012). Cranes distributed in three relatively separate areas of Yangmeishan-Baijiacun-Lijiawan (YBL), Nugexun-Dideka (ND) and Dideka-Daqiao (DD) in our study area (Fig. 1), *nigricollis* and *grus* both occurred in YBL and ND area while only *grus* was located in DD area

(Kong et al., 2018). The YBL area is surrounded by seven villages of c. 2,000 people and the ND area has a human population of c. 800, while the area situated between Dideka and Daqiao (DD area) is far from human settlements (Fig. 1). No cranes were hunted by natural predators in this area, humans are the only potential threats for these birds; and sometimes the smaller *grus* face attack and exclusion by *nigricollis* (Kong et al., 2018). With a mean annual temperature of 9.6 °C, this area experiences a 45-days long freeze-up period in winter (Qiou and Yang, 2012).

## 2.2. Data collection

Field surveys crossed the whole wintering period from November 2010 to March 2011. In winter, cranes share a common roost site along the lake shore at night and foraging in surrounding areas in daytime (Kong et al., 2018). We located each crane group along a line transect of 30 km on clear days without rain, snow or strong wind during 07:00–19:00 (Kong et al., 2018). Instantaneous scan sampling with 3-min interval was used to collect behavior data for every focal group (Kong et al., 2008; Xu et al., 2013). Observation ceased when group size changed or cranes were out of sight. We focus on vigilance behavior referring to head up with neck stretched while standing, walking or lying down (Kong et al., 2008, 2011). Meanwhile other behaviors including foraging, preening, locomotion and fight were also recorded so as to understand how time was allocated to each kind of behavior as a whole. Foraging refers to feeding and head down searching. Preening contains nursing and washing feather, resting, dancing and singing. Locomotion only means wandering without head up and short distance flying in a focal group. Fight means direct contest with intruders or other species in a group (Kong et al., 2008, 2011). For each group, we also recorded the habitat they occupied and three habitat types of farmland, grassland, and marsh were recognized. Farmland is ploughed or unploughed croplands of *Solanum tuberosum*, *Brassica campestris*, and *Zea mays*. Grassland is dry meadow areas usually on the hillside covered by *Leontopodium andersonii*, *Primula malacoides* and *Trifolium repens*. Marsh is flooded area with shallow water of  $\leq 50$  cm along the reservoir (Kong et al., 2018).

## 2.3. Data process and statistic

Time budget of each activity was measured as the percentage of individuals engaging in group behavior. All groups observed were taken into the time budget calculation while only groups with at least three scan samplings (or 6 min observation session) were used to detect variable effects on vigilance behavior. Vigilance related variables of group scan level and group scan frequency were calculated for each group. We defined the percentage of individuals engaged in alert scanning in the group as group scan level and the percentage of intervals during which at least one crane was vigilant as group scan frequency during the observation session (Xu et al., 2013). As group size was significantly correlated with crane vigilance (Xu et al., 2013; Yang et al., 2016), we only took family groups with two adults and 0–2 juveniles (group size from 2 to 4 individuals) into consideration in our study in order to avoid or weaken this effect. It is difficult to distinguish male from female in the field, as adult cranes are similar in both body size and plumage color, but it is easy to recognize the first-winter juvenile with mottled, light yellow or brown plumage (Johnsgard, 1983). Although juveniles showed lower vigilance than adults, they still spent about 10% of time scanning (Wang et al., 2009; Ge et al., 2011), which is not negligible and contributed to collective vigilance. Thus, we also considered juvenile behaviors in our study. Previous studies have reported that cranes showed daily and seasonal fluctuations in behavior (Kong et al., 2008), so we classified daily time into 12-time intervals with 1 h-interval from 07:00 to 19:00 and five months were set (Nov., Dec., Jan., Feb. and Mar.). As habitat type was proven to have a significant effect on crane behavior (Kong et al., 2011), we recorded

behavioral data in three habitat types of farmland, grassland and marsh as mentioned. As to the distribution areas of YBL, ND and DD mentioned, nearly 99% of *nigricollis* located in YBL and ND areas and *grus* distributed in all three areas (Kong et al., 2018, Fig. 1), we considered co-occurrence areas of *grus* and *nigricollis* in two levels and also the other DD area only for *grus*. We found the cranes, especially *grus* often mixed with other species (e.g. Bar-headed Goose *Anser indicus*) (Luo, 2012). So, group composition status (mixed or unmixed) for each group was also recorded.

We ran one-sample Kolmogorov-Smirnov test to check the normality of each data set. We tried to conduct normality transformation for the response variables, e.g., the data for time budget, group scan frequency and group scan level were arcsine square root transformed, but failed. So parametric and non-parametric tests were adopted in our study as appropriate. Generalized linear model was used to distinguish main and factor effects of each effect variable, including month (five levels), time (twelve levels), habitat type (three categories), distribution area (two levels in co-occurred area of YBL and ND; for *grus* in the area of DD without *nigricollis*, this variable was excluded in the model), group composition status (two levels) and group size (three levels) for response variables (group scan level and group scan frequency) of both species (Li et al., 2012). We also tested the species effect (with single-species data without mixing with other species) in areas where both species were present; other variables showing significant effects, including time, distribution area and group size, were also included in the analysis (see the Results). Generalized linear model was also used to distinguish mixed group variables effects (mixed group category and group size) on *grus* vigilance in mixed groups. For each model analysis, we set group size as covariate in order to control group size effect. We filtered variables with significant main effect on vigilance by taking all variables into consideration; the filtered variables were then introduced into the model again to test both main and factor effects on response variables. For paired data comparison, we selected *t*-test and non-parametric Mann-Whitney *U* test in this study and the two tailed probability of  $< 0.05$  was considered as significant differences. All statistics were estimated using IBM SPSS 20.0.

## 3. Results

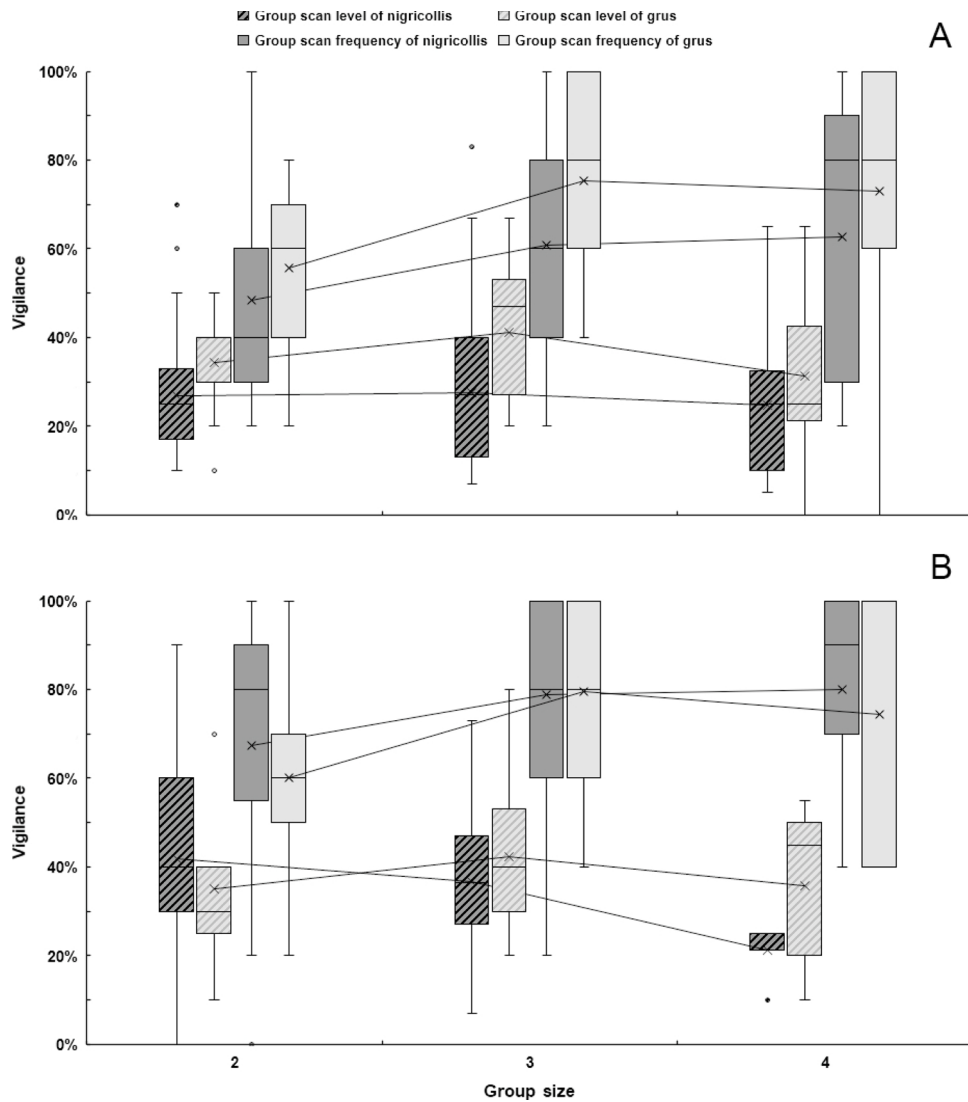
We recorded 375 groups of *G. nigricollis* and 174 groups of *G. grus*. We obtained 5,501 min observations for 306 *nigricollis* groups (on average 18 min per group, range 6–75 min) and 2,340 min observations for 138 *grus* groups (17 min per group, range 15–60 min) after excluding groups with observation sessions less than 6 min. In total, *grus* spent significantly more time vigilant ( $z = -5.538$ ,  $p = 0.000$ ) and less time preening ( $z = 5.828$ ,  $p = 0.000$ ) than *nigricollis*, while no significant differences were found for foraging, locomotion and fight between species (Table 1).

We detected significant species effects on group scan level ( $\chi^2 = 8.199$ ,  $p = 0.004$ ,  $df = 1$ ), group size effect on group scan frequency ( $\chi^2 = 15.941$ ,  $p = 0.000$ ,  $df = 1$ ), and a significant distribution area effect for both (level:  $\chi^2 = 22.869$ ,  $p = 0.000$ ,  $df = 1$ ; frequency:

**Table 1**  
Time budget comparison of sympatric *Grus grus* and *G. nigricollis*.

Behaviors	<i>G. nigricollis</i> (Mean $\pm$ SD, n = 375)	<i>G. grus</i> (Mean $\pm$ SD, n = 174)	t / Z *	p
Foraging	57.7 % $\pm$ 24.3 %	55.0 % $\pm$ 25.5 %	1.185	0.236
Vigilance	27.9 % $\pm$ 16.5 %	37.3 % $\pm$ 20.2 %	-5.208	0.000
Preening	12.4 % $\pm$ 19.0 %	4.6 % $\pm$ 12.1 %	-6.442	0.000
Locomotion	2.0 % $\pm$ 6.1 %	3.1 % $\pm$ 8.8 %	-1.581	0.115
Fight	0.1 % $\pm$ 0.4 %	0.0 % $\pm$ 0.0 %	0.819	0.413

\* as the vigilance and preening data violate normality, non-parametric Mann-Whitney *U* test was used, while mean comparison of foraging, locomotion and fight were estimated with *t*-test.



**Fig. 2.** Vigilance of *Grus grus* and *nigricollis* in different groups in their common distribution area of Yangmeishan-Baijiacun-Lijiawan (YBL, Fig. 2A), Nugexun-Dideka (ND, Fig. 2B). Box plots show medians, quartiles and 5- and 95-percentiles, and the trendline (the blackline) of mean (the “x” symbol).

$\chi^2 = 28.465$ ,  $p = 0.000$ ,  $df = 1$ ; Fig. 2) in the areas of co-occurrence of YBL and ND. Each species had the highest vigilance performance in the ND area and the lowest vigilance in the YBL area (see Appendix Table A1).

For both species, group size was significantly positively related to group scan frequency (*nigricollis*:  $\chi^2 = 20.362$ ,  $p = 0.000$ ,  $df = 1$ ; *grus* in YBL & ND area:  $\chi^2 = 13.410$ ,  $p = 0.000$ ,  $df = 1$ ; *grus* in DD area:  $\chi^2 = 7.100$ ,  $p = 0.008$ ,  $df = 1$ ), and a negative correlation with group scan level ( $p > 0.05$ , see Appendix Tables A2, A3 for details; Fig. 2).

Moreover, distribution area was significantly correlated with both group scan frequency ( $\chi^2 = 18.888$ ,  $p = 0.000$ ,  $df = 1$ ) and level ( $\chi^2 = 19.285$ ,  $p = 0.000$ ,  $df = 1$ ) of *nigricollis* (Fig. 2). While time of day (frequency:  $\chi^2 = 21.576$ ,  $p = 0.017$ ,  $df = 10$ ; level:  $\chi^2 = 36.627$ ,  $p = 0.000$ ,  $df = 10$ ) and group composition status (frequency:  $\chi^2 = 10.960$ ,  $p = 0.001$ ,  $df = 1$ ; level:  $\chi^2 = 17.369$ ,  $p = 0.000$ ,  $df = 1$ ) was significantly correlated with group scan frequency and level of *grus*

when co-occurring with *nigricollis*; but when *nigricollis* was absent, time was not correlated with *grus* vigilance ( $p > 0.05$ , Appendix Table A2). We detected significantly fluctuating vigilance of *grus* throughout the day, with obvious peaks in the morning and the afternoon with a minimum at noon, while vigilance for *nigricollis* was stable (Fig. 3).

The interaction between group size and composition status was correlated with group scan frequency of *grus* ( $\chi^2 = 4.015$ ,  $p = 0.045$ ,  $df = 1$ ). For each family type, *grus* elevated vigilance (both scan frequency and level) in groups without the other species (Fig. 4).

#### 4. Discussion

By taking ecological factors into consideration, we studied vigilance of sympatric *Grus grus* and *G. nigricollis*, which could increase our understanding of how vigilance behavior was related in a common and a threatened crane species. Our results indicated that common *grus* are



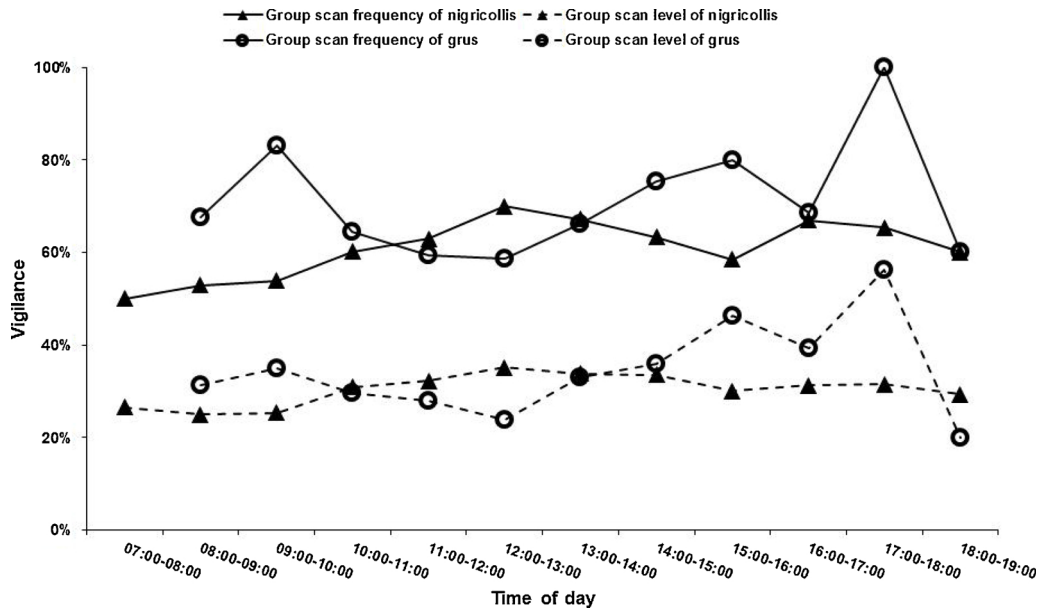


Fig. 3. Daily vigilance rhythm of *Grus grus* and *G. nigricollis*.

more alert and more flexible in antipredator strategy than the threatened *nigricollis*. Another study conducted in Yancheng reserve, eastern China also demonstrated that common *Grus grus* were more vigilant than sympatric threatened *Grus japonensis* (Ge et al., 2011). Antipredator strategies of *grus* included decreasing time allocation to preening, foraging with other species to form large flocks, alternating with foraging time rhythm when facing interspecific competition (Luo, 2012) or even utilized areas (55% of *grus* population) without *nigricollis*

(Kong et al., 2018), so as to maintain relatively high levels of alertness while sustaining foraging time allocation (Table 1).

Group scan frequency can be recognized as collective vigilance; and as calculated from vigilant individual percentage in groups, group scan level is also equal to individual vigilance (Elgar, 1989; Roberts, 1996). With increasing group, more individuals could engage in scanning and leave less time for alert gaps, leading to an increase in collective scan frequency (collective vigilance), while every group member could

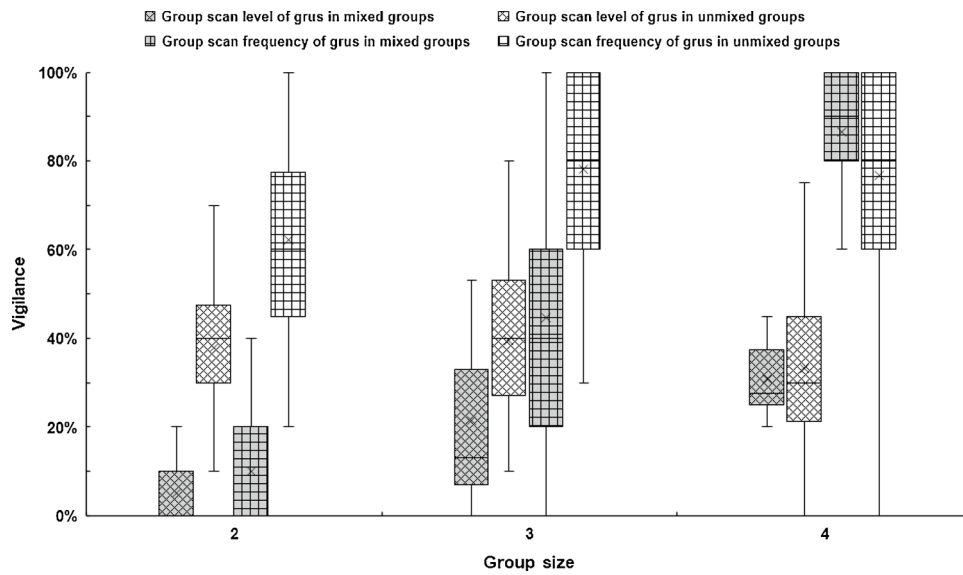


Fig. 4. Vigilance of *Grus grus* in mixed and unmixed groups. Box plots show medians, quartiles and 5- and 95-percentiles. “×” symbol in the boxes indicates mean.

decrease scan rate (individual vigilance), named the “many eyes effect” (Pulliam, 1973). Although we restricted the objective of our study to family groups of 2–4 members, we detected a significant group effect on vigilance for both *grus* and *nigricollis* (an increase in scan frequency and a weak decline in scan level; Fig. 2). This is because juveniles behaved more like adults contributing to group vigilance even when they are still young (Wang et al., 2009; Ge et al., 2011). Empirical and theoretical studies were consistent with the group size effect hypothesis, this could also be tested even in small groups (Pulliam, 1973; Caraco et al., 1980), such as family groups in our study.

In our study, we found both group scan frequency and scan level of *nigricollis* to be correlated with distribution area, but without any impact from other environmental factors, e.g. month, time of the day and habitat type. Moreover, *nigricollis* in the ND area with higher group scan level and frequency than that of the YBL area (Fig. 2; Appendix Table A1), implying higher disturbance in the ND area. Though more villages and residents are distributed around YBL than ND, the main habitat type of marsh limited human accessibility to YBL, while farmland in ND area provided easy approach for human beings (Qiou and Yang, 2012; Kong et al., 2018). Correspondingly, *nigricollis* selected YBL area the most and was recognized as the kernel distribution area (50–70% isopleths of utilization) of cranes; whereas, the ND area was selected by *nigricollis* as marginal area (90% isopleths of utilization; Fig. 1) as our former study reported (Kong et al., 2018). Consistent with *nigricollis*, *grus* showed higher vigilance in the ND area (Fig. 2; Appendix Table A1), providing higher disturbance in this area. Because *grus* maintained high vigilance level across the whole study area, no significant distribution area effect was detected for *grus* vigilance.

*grus* was more affected by group composition status and time of day than *nigricollis*. By foraging with other species, such as Bar-headed Goose *Anser indicus* and also *nigricollis*, *grus* could obtain more benefits from large groups (Caraco et al., 1980) and decrease scan frequency and scan level (Fig. 4; Appendix Fig. A1). Further analysis indicated that vigilance in *grus* depended on mixed group size (group scan frequency:  $\chi^2 = 3.723$ ,  $p = 0.054$ ,  $df = 1$ ) rather than mixed group category (group scan frequency:  $\chi^2 = 4.674$ ,  $p = 0.097$ ,  $df = 2$ ; Appendix Table A3) consistent with the group size effect hypothesis.

Generally, animal vigilance behavior and rhythm may be restricted to the predominant behavior of foraging (Pravosudov and Grubb, 1997). Diurnal animals e.g. cranes, usually need to refuel energy lost during the nocturnal fasting period and have morning and / or afternoon foraging peaks (McNamara and Houston, 1986; Kong et al., 2008), so energy reserves (body mass) for the night steadily accumulate through the day (Pravosudov and Grubb, 1997). If energy accumulation is sufficient for the coming night, animals achieve this by having a low foraging rate and high vigilance rate (McNamara and Houston, 1986; Pravosudov and Grubb, 1997). When we checked the foraging rhythm of *grus* in our study, we found significant fluctuations and a steady decrease throughout the day (Appendix Fig. A2), obvious vigilance fluctuations and an ascending trend was detected, implying that *grus* vigilance was influenced by time of day (Appendix Table A2). In the DD area, where the larger *nigricollis* is absent, both group scan frequency and scan level of *grus* were unaffected by time, indicating inter-specific

competition in areas of co-occurrence. Our previous studies suggested that these two species could utilize segregated areas (Kong et al., 2018) and forage at different times in the same area (Luo, 2012) to alleviate competition. Season could partly correlate with time effects on *grus* scan frequency in the DD area (Appendix Table A2). As for *nigricollis*, we found both foraging and vigilance behavior of *nigricollis* to remain stable throughout the day (Appendix Fig. A2).

Thus, sympatric *grus* and *nigricollis* adopted different vigilance behavior when taking ecological factors into consideration. Vigilance behavior of the threatened larger *nigricollis* was mainly affected by group size and distribution area (disturbance). While group size, group composition status (actual effect is mixed group size), time of day (foraging rhythm) and species (inter-specific competition) effects on *grus* vigilance were detected. Thus, common *grus* showed higher vigilance than threatened *nigricollis*, but *grus* had similar foraging activity with *nigricollis*, by reducing allocation to preening. Hence, we argue that keeping vigilant may partly contribute to population increase in common *grus*; lower vigilance of threatened *nigricollis* may suffer high predation risk (Chen, 1994) resulting in population decline.

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## CRediT authorship contribution statement

**Dejun Kong:** Conceptualization, Methodology, Formal analysis, Writing - original draft, Writing - review & editing. **Weixiong Luo:** Investigation, Data curation. **Anders Pape Møller:** Writing - review & editing. **Yanyun Zhang:** Software, Formal analysis, Writing - review & editing. **Xiaojun Yang:** Conceptualization, Methodology, Writing - review & editing.

## Declaration of Competing Interest

All authors declare that they have no competing interests.

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**Table A1**

Group scan level and frequency of *Grus grus* and *G. nigricollis* in different areas. YBL, ND and DD indicate Yangmeishan-Bajiacun-Ljiawan, Nugexun-Dideka and Dideka-Daqiao, respectively. *N* is the sample size and the three figures in the bracket are sample size of difference family groups of 2, 3 and 4 individuals; bold figures mean significant difference ( $p < 0.05$ ).

Species	Distribution area	Group scan level Mean ± SD	Group scan frequency Mean ± SD	<i>N</i>
<i>Grus grus</i>	YBL	29.31 % ± 18.46 %	60.42 % ± 31.60 %	64 (16/22/26)
	ND	38.03 % ± 18.35 %	74.65 % ± 28.37 %	35 (5/21/9)
	DD	35.36 % ± 16.60 %	77.69 % ± 23.78 %	39 (5/21/13)
	One-way ANOVA LSD	$F = 3.058, p = 0.050, df = 2$ YBL vs ND: $p = 0.022$ ; YBL vs DD: $p = 0.099$ ; ND vs DD: $p = 0.523$		$F = 5.299, p = 0.006, df = 2$ YBL vs ND: $p = 0.020$ ; YBL vs DD: $p = 0.004$ ; ND vs DD: $p = 0.651$
<i>Grus nigricollis</i>	YBL	27.44 % ± 27.16 %	56.27 % ± 26.27 %	200 (96/89/15)
	ND	36.48 % ± 27.16 %	70.82 % ± 27.16 %	106 (48/53/5)
	DD	—	—	0
	Mann-Whitney <i>U</i> test	YBL vs ND: $Z = -4.257, p = 0.000$		YBL vs ND: $Z = -4.572, p = 0.000$

**Table A2**

Statistical outputs of generalized linear model for testing effect variables on vigilance behavior (group scan frequency and level) of *Grus nigricollis*. Bold figures mean significant difference ( $p < 0.05$ ).

Effects	Variables	Group scan frequency			Group scan level		
		$\chi^2$	<i>df</i>	<i>p</i>	$\chi^2$	<i>df</i>	<i>p</i>
Main effects	Month	8.855	4	0.065	7.018	4	0.135
	Time of day	10.982	11	0.445	11.541	11	0.399
	Habitat type	0.414	1	0.520	0.415	1	0.519
	Distribution area	18.888	1	<b>0.000</b>	19.285	1	<b>0.000</b>
	Group composition status	0.054	1	0.817	0.324	1	0.569
	Group size	20.362	1	<b>0.000</b>	1.248	1	0.264
Factor effects	Distribution area	0.311	1	0.577	—	—	—
	Group size	17.943	1	0.000	—	—	—
	Distribution area × Group size	0.258	1	0.611	—	—	—

**Table A3**

Statistical outputs of generalized linear model for testing effect variables on vigilance behavior (group scan frequency and level) of *Grus grus*. Bold figures mean significant difference ( $p < 0.05$ ). YBL, ND and DD indicate Yangmeishan-Bajiacun-Ljiawan, Nugexun-Dideka and Dideka-Daqiao, respectively. \* means inadequate sample for subsequent factor effect modeling.

Distribution Area	Effects	Variables	Group scan frequency			Group scan level		
			$\chi^2$	<i>df</i>	<i>p</i>	$\chi^2$	<i>df</i>	<i>p</i>
YBL and ND area	Main effects	Month	3.130	4	0.536	2.751	4	0.600
		Time of day	21.576	10	<b>0.017</b>	36.627	10	<b>0.000</b>
		Habitat type	3.407	2	0.182	3.972	2	0.137
		Distribution area	0.109	1	0.741	0.279	1	0.597
		Group composition status (GCS)	10.960	1	<b>0.001</b>	17.369	1	<b>0.000</b>
		Group size	13.410	1	<b>0.000</b>	0.083	1	0.773
	Factor effects	Time of day	2.642	7	0.916	31.985	10	0.000
		GCS	10.146	1	0.001	23.939	1	0.000
		Group size	15.360	1	0.000	—	—	—
		Time of day × GCS	5.214	4	0.266	11.586	8	0.171
		Time of day × Group size	6.446	7	0.489	—	—	—
		GCS × Group size	4.015	1	<b>0.045</b>	—	—	—
		Time of day × GCS × Group size	5.630	4	0.229	—	—	—
DD area	Main effects	Month	9.896	3	<b>0.019</b>	5.710	3	0.127
		Time of day	6.193	8	0.626	7.696	8	0.464
		Habitat type	0.091	1	0.763	1.668	1	0.197
		GCS*	12.095	1	<b>0.001</b>	4.729	1	<b>0.030</b>
		Group size	7.100	1	<b>0.008</b>	0.063	1	0.802
	Factor effects	Month	16.241	1	0.000	—	—	—
		Group size	4.916	1	0.027	—	—	—
		Month × Group size	9.369	1	<b>0.002</b>	—	—	—



**Table A4**  
Statistical outputs of general linear model for testing mixed group effect variables on vigilance behavior (group scan frequency and level) of *Grus grus*.

Variables	df	Group scan frequency		Group scan level	
		$\chi^2$	P	$\chi^2$	p
Mixed group category	2	4.674	0.097	4.619	0.099
Mixed group size	1	3.723	0.054	2.561	0.110
Mixed group category $\times$ Mixed group size	2	5.289	0.071	3.810	0.149

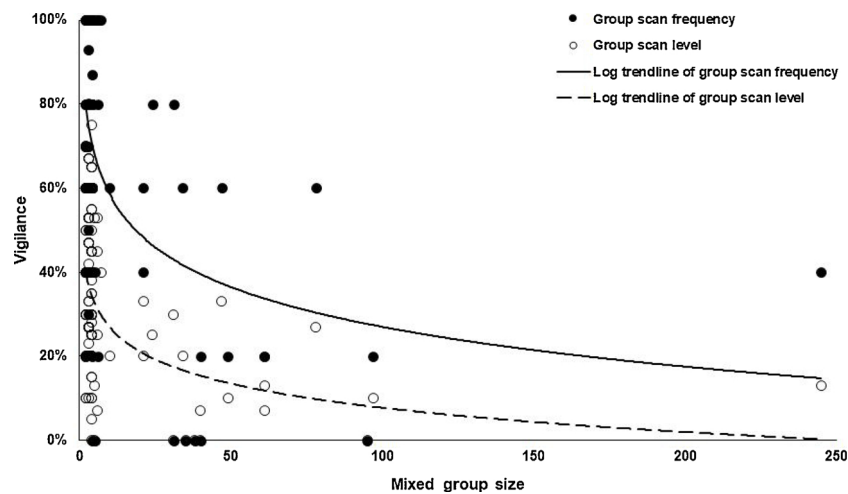


Fig. A1. Mixed group size effects on vigilance behavior of *Grus grus*.

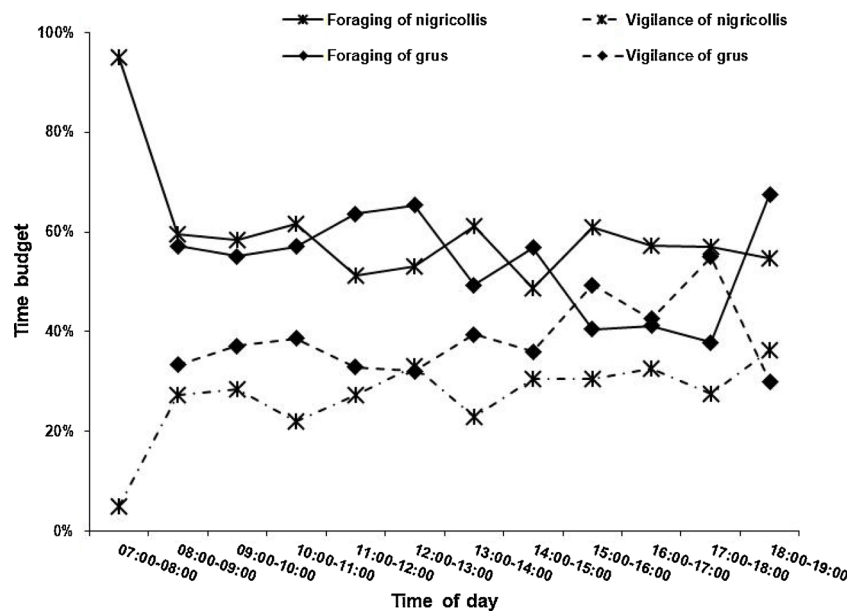


Fig. A2. Daily foraging and vigilance rhythm of *Grus grus* and *G. nigricollis*.

**References**

Beauchamp, G., 2015. *Animal Vigilance: Monitoring Predators and Competitors*. Academic Press, San Diego, CA.  
 Bertram, B.C.R., 1978. Living in groups: predators and prey. In: Krebs, J.R., Davies, N.B. (Eds.), *Behavioural Ecology: An Evolutionary Approach*. Blackwell Scientific Publications, Oxford, pp. 64–96.  
 Caraco, T., Martindale, S., Pulliam, H.R., 1980. Avian flocking in the presence of a predator. *Nature* 285 (5), 400–401.

Caro, T.M., 2005. *Antipredator Defenses in Birds and Mammals*. University of Chicago Press, Chicago.  
 Chen, X.P., 1994. Black-necked Cranes and the natural and social conditions of their wintering areas in Xundian County. *Yunnan Environ. Sci.* 13 (1), 45–47.  
 Cooper Jr., W.R., Blumstein, D.T., 2015. Escape behavior: importance, scope, and variables. In: Cooper Jr.W.R., Blumstein, D.T. (Eds.), *Escape from Predators: An Integrative View of escape Decisions*. Cambridge University Press, Cambridge.  
 Dugatkin, L.A., 2004. *Principles of Animal Behavior*. W.W. Norton & Company, Inc., New York.

- Elgar, M.A., 1989. Predator vigilance and group size in mammals and birds: a critical review of the empirical evidence. *Biol. Rev.* 64, 13–33.
- Ge, C., Beauchamp, G., Li, Z.Q., 2011. Coordination and synchronisation of anti-predation vigilance in two crane species. *PLoS One* 6 (10), e26447. <https://doi.org/10.1371/journal.pone.0026447>.
- IUCN, 2019. The IUCN Red List of Threatened Species. Version 2019-2. <http://www.iucnredlist.org>. Downloaded on 18 July 2019. .
- Jiang, Y.T., Møller, A.P., 2017a. Antipredator escape distances of common and threatened birds. *Behav. Ecol.* 28 (6), 1498–1503.
- Jiang, Y.T., Møller, A.P., 2017b. Escape from predators and genetic variance in birds. *J. Evol. Biol.* 30, 2059–2067.
- Johnsgard, P.A., 1983. *Cranes of the World*. Indiana University Press, Bloomington, USA.
- Kong, D.J., Yang, X.J., Liu, Q., Zhong, X.Y., Yang, X.J., 2008. Diurnal time budget and behavior rhythm of wintering black-necked crane (*Grus nigricollis*) at Dashanbao in Yunnan. *Zool. Res.* 29 (2), 195–202.
- Kong, D.J., Yang, X.J., Liu, Q., Zhong, X.Y., Yang, X.J., 2011. Winter habitat selection by the vulnerable black-necked crane *Grus nigricollis* in Yunnan, China: implications for determining effective conservation actions. *Oryx* 45 (2), 258–264.
- Kong, D.J., Luo, W.X., Liu, Q., Li, Z.Q., Huan, G.Y., Zhang, J.J., Yang, X.J., 2018. Habitat use, preference, and utilization distribution of two crane species (Genus: *Grus*) in Huize National Nature Reserve, Yunnan–Guizhou Plateau, China. *PeerJ* 6, e5105.
- Krajewski, C., Sipiowski, J.T., Anderson, F.E., 2010. Complete mitochondrial genome sequences and the phylogeny of cranes (Gruiformes: gruidae). *Auk* 127 (2), 440–452.
- Li, C.L., Jiang, Z.G., Li, C.L., Li, Z.Q., Fang, H.X., Li, C.W., Beauchamp, G., 2012. Effects of reproductive status, social Rank, sex and group size on vigilance patterns in Przewalski's gazelle. *PLoS One* 7 (2), e32607.
- Li, Z.Q., Wang, Z., Ge, C., 2013. Time budget of wintering red-crowned cranes: effects of habitat, age and family size. *Wetlands* 33 (2), 227–232.
- Li, C.L., Beauchamp, G., Wang, Z., Cui, P., 2016. Collective vigilance in the wintering hooded crane: the role of flock size and anthropogenic disturbances in a human-dominated landscape. *Ethology* 122, 999–1008.
- Lima, S.L., 1990. The influence of models on the interpretation of vigilance. In: Interpretation and explanation in the study of animal behaviour. In: BekoV, M., Jamieson, D. (Eds.), *Explanation, Evolution and Adaptation* Vol. 2. Westview Press, Boulder, Colorado, pp. 246–267.
- Luo, W.X., 2012. Wintering Ecology and Coexistence Mechanism of Black-necked Cranes (*Grus nigricollis*) and Common Cranes (*Grus Grus*) at Huize. A Dissertation Submitted to Graduate University of Chinese Academy of Sciences. Kunming Institute of Zoology, Chinese Academy of Science, Yunnan, China.
- Mcnamara, J.M., Houston, A.I., 1986. The common currency for behavioral decisions. *Am. Nat.* 127, 358–378.
- Møller, A.P., 2008. Flight distance and population trends in European breeding birds. *Behav. Ecol.* 19, 1095–1102.
- Møller, A.P., Samia, D.S.M., Weston, M.A., Guay, P.-J., Blumstein, D.T., 2014. American exceptionalism: population trends and flight initiation distances in birds from three continents. *PLoS One* 9 (9), e107883. <https://doi.org/10.1371/journal.pone.0107883>.
- Powell, G.V.N., 1974. Experimental analysis of the social value of flocking by starlings (*Sturnus vulgaris*) in relation to predation and foraging. *Animal Behav.* 22, 501–505.
- Pravosudov, V.V., Grubb JR., T.C., 1997. Management of fat reserves and food caches in Tufted Titmice (*Parus bicolor*) in relation to unpredictable food supply. *Behav. Ecol.* 8, 332–339.
- Pulliam, H.R., 1973. On the advantages of flocking. *J. Theor. Biol.* 38, 419–422.
- Pulliam, H.R., Pyke, G.H., Caraco, T., 1982. The scanning behaviour of juncos: a game-theoretical approach. *J. Theor. Biol.* 95, 89–103.
- Yunnan Huize National Nature Reserve of Black-Necked Crane. In: Qiou, G.X., Yang, X.J. (Eds.), *Yunnan Science and Technological Press House, Kunming, China*, pp. 1–5.
- Roberts, G., 1996. Why individual vigilance declines as group size increases. *Animal Behav.* 51, 1077–1086.
- Thaxter, C.B., Joys, A.C., Gregory, R.D., Baillie, S.R., Noble, D.G., 2010. Hypotheses to explain patterns of population change among breeding bird species in England. *Biol. Conserv.* 143, 2006–2019.
- Tyrrell, L.P., Fernández-Juricic, E., 2015. Sensory systems and escape behavior. In: Cooper Jr.W.E., Blumstein, D.T. (Eds.), *Escaping from Predators: An Integrative View of Escape Decisions*. Cambridge University Press, Cambridge, U.K, pp. 322–342.
- Wang, K., Yang, X.J., Zhao, J.L., Yu HZ, Min L., 2009. Relations of daily activity patterns to age and flock of wintering black-necked crane at Napa Lake, Shangri-La in Yunnan. *Zool. Res.* 30 (1), 74–82.
- Wang, Z., Li, Z.Q., Beauchamp, G., Jiang, Z.G., 2011. Flock size and human disturbance affect vigilance of endangered red-crowned cranes (*Grus japonensis*). *Biol. Conserv.* 144, 101–105.
- Xia, C.J., Xu, W.X., Yang, W.K., Blank, D., Qiao, J.F., Liu, W., 2011. Seasonal and sexual variation in vigilance behavior of goitered gazelle (*Gazella subgutturosa*) in western China. *J. Ethol.* 29 (3), 443–451.
- Xu, F., Ma, M., Yang, W.K., Blank, D., Ding, P., Zhang, T., 2013. Vigilance in Black-necked Cranes: effects of predation vulnerability and flock size. *The Journal of Wilson Ornithology* 125 (1), 208–212.
- Yang, L., Zhuom, C.J., Li, Z.Q., 2016. Group size effects on vigilance of wintering black-necked cranes (*Grus nigricollis*) in Tibet, China. *Waterbirds* 39 (1), 108–113.