Bird Study
Publication details, including instructions for authors and subscription information:
http://www.tandfonline.com/loi/tbis20

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Published online: 25 Jun 2015.

Bird Study (2015), 1–5
http://dx.doi.org/10.1080/00063657.2015.1047736

SHORT REPORT

Group size and disturbance effects on group vigilance in the Great Bustard *Otis tarda* in western China

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Capsule Great Bustards *Otis tarda* gained vigilance benefits from increasing group size: they showed a negative correlation between group size and the percentage of individuals scanning, and a positive correlation between group size and the percentage of time with at least one individual scanning. The relationship between vigilance and group size was independent of level of disturbance but individual vigilance was higher closer to a road. Higher group size and provision of continuous areas of high-quality habitat away from disturbance allows Great Bustards to reduce individual vigilance and so potentially increase investment in feeding time and their survival.

Vigilance is often assumed to be a response to potential predation risk, and living in a group provides members with potential benefits with respect to vigilance. One major advantage is the decrease in the allocation of time dedicated to vigilance within a larger group, which is called the 'group size effect' (Pulliam 1973). This phenomenon has been reported in many bird and mammal species (Elgar 1989, Dias 2006), and three main hypotheses have been proposed to explain this negative correlation: the 'many-eyes' effect, where more individuals are available to detect predators (Pulliam 1973); the risk-dilution effect, where increasing number of individuals in a group dilute the risk of any one individual being attacked (Hamilton 1971, Cresswell 1994); and the 'scramble competition' hypothesis, when competition for limited resources leads to a decrease in time that can be allocated to vigilance (Beachamp & Ruxton 2003).

It is crucial to measure collective vigilance to fully understand the benefits that grouping confers to each individual, because group members are assumed to be more vulnerable to predation when no one in the group is vigilant (Pays *et al.* 2012). That large groups benefit from an increase in collective vigilance has been reported by several researchers (Bertram 1980, Elgar & Catterall 1981, Ebensperger *et al.* 2006), but it is not the case for all birds and mammals (Pays & Jarman 2008). For example with the Greater Rhea *Rhea americana*, the group size effect only decreases an individual's vigilance without affecting collective vigilance (Martella *et al.* 1995, Fernández *et al.* 2003).

Apart from group size, predation risk is another major selection pressure that determines the vigilance behaviour of animals (Hunter & Skinner 1998, Lima 1998). For example, Przewalski's Gazelles *Procapra przewalskii*, increases their level of vigilance under threat of high predation (Li *et al.* 2009). However, such relationships between vigilance and the risk of predation have not always been found (Cameron & Du Toit 2005). Distance to predator concealing cover or refugee is frequently used as a measure of predation risk (Riddington *et al.* 1996, Pays *et al.* 2012) and so incorporation of this potentially confounding measure into vigilance studies, particularly when group size may co-vary with distance to cover, may help to reveal the true group-size effect on vigilance.

Habitat type may also affect vigilance behaviour of birds. For species that rely on detecting predators by sight (Lima & Dill 1990), increased visual obstruction has been shown to increase vigilance in many taxa

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(Elgar 1989). For example, Lesser Rheas *Rhea pennata pennata*, tend to be more vigilant in areas with low visibility, which also hinder escape by running (Barri *et al.* 2012), and the collective vigilance of Guanacos *Lama guanicoe* was observed to increase with the number of adults in closed habitats (Marino & Baldi 2008). For birds living in farmland areas, the habitat structure (choice of crop type, timing of harvest and ploughing) is potentially easy to manipulate, so there may be important effects of changes in farming techniques that impact on vigilance levels and so foraging time budgets (Whittingham *et al.* 2004).

Great bustards *Otis tarda*, a species highly susceptible to disturbance, inhabit agro-ecosystems, within which the intensification of agricultural development and human-induced habitat fragmentation have led to a decline in their numbers (Alonso & Palacín 2010). Living in such anthropogenically modified habitats at lower densities can make animals more susceptible to further population declines because they lose the advantages of group vigilance (Watson *et al.* 2007). Human disturbance might therefore particularly be expected to influence vigilance and so foraging behaviour in these species, and so any potential advantages gained by the group-size effect on vigilance may be crucial for individual time budgets and so survival and population dynamics. However, vigilance behaviour in the Great Bustard has only rarely been studied (Sastre *et al.* 2009). In this paper, we examined how vigilance changed with group size in the Great Bustard, and determined whether this relationship was influenced by disturbance risk (as a proxy for perceived predation risk) or habitat type.

Field research was carried out in the vicinity of the city of Tacheng, Xinjiang, China. This area probably holds the highest density Great Bustard population in China with around 300 birds located in three concentrated distribution areas of 1500 km^2, where birds congregate before migration (unpubl. data). These areas are traditional agricultural areas, consisting mostly of a mosaic of cereals (mostly wheat and corn), ploughed fields and fallow lands. Most cereal crops are grown in a two-year rotation system. Every year from October to November Great Bustards gather here before migration, with most feeding in the stubble wheat fields on wheat seeds, or more rarely in the winter wheat fields eating the wheat seedlings.

Observations were conducted using the group scan sampling method (Martin & Bateson 1993) from 11 to 20 October 2014 from 7:00 to 19:30 hours. Target groups were randomly selected and observed using a telescope (20 × 60). Each group was observed only once in a day. Because it was difficult to identify individuals, we avoided group re-sampling by observing the groups over a long distance, allowing us to ensure spatial independence between groups sampled in the same day. Observation was conducted in different locations (three concentrated distribution areas) with a three day rotation. We attempted to observe the bustards over all daylight hours equally, in order to minimize the effect of any diurnal variation in vigilance.

One session was defined as starting when a group was first found until the group size changed or the group left the area. We distinguished vigilance behaviour as when a Great Bustard had its head up while standing erect or scanning its surroundings (Martínez 2000). The activities of each group member were recorded at 5-minute intervals, with all observations being carried out by the same person. Actual observation time ranged from 30 to 105 minutes, with an average of 36.7 minutes. In total, we collected data from 102 groups of Great Bustards gaining 3740 minutes of observations. The range of observed group sizes fluctuated from 2 to 25 individuals, although most groups contained less than 10 birds. Groups containing more than 10 were pooled into one group (defined as 11) due to their limited number. Individuals were defined as members of the same group if distances between them were less than 50 m (Fernández *et al.* 2003). Group scan level (individual vigilance) was calculated as the percentage of individuals within the group that were engaged in scanning behaviour during a session. Group scan frequency (group vigilance or collective detection) was measured as the proportion of time that at least one bird of the group was vigilant (Fernández *et al.* 2003).

Great bustards are highly sexually dimorphic, polygynous birds, with adult males being much bigger than females and sub-adults. This size difference made it easy to distinguish adult males from a distance (Alonso *et al.* 2009), however, since a significant proportion of females and sub-adults could not be distinguished during this period, we did not consider different categories of individuals in our analysis. Since Great Bustards were found in two habitat categories in our study area, agricultural fields of winter wheat and stubble wheat, we considered the type of habitat as an environmental factor potentially affecting vigilance. In addition, we considered different levels of human disturbance, as a proxy for predation risk, corresponding to various distances groups were from the road that crossed the study area, namely, less than 100 m, 100–300 m and more than 300 m.

Table 1. Results of GLMs to test variation in proportion of individuals scanning (Individual level) and proportion of the time that at least one individual was scanning (Group level) with group size, distance to road and habitat type. The individual level model was highly significant ($F_{4,97}$ = 11.4, $P < 0.001$, adjusted $R^2 = 0.29$). The group level model was highly significant ($F_{4,97} = 10.5$, $P < 0.001$, adjusted $R^2 = 0.27$). The intercept for both models was winter wheat and <100 m from the road.

		Individual level			Group Level		
Source	df	*t*	*P*	Est.	*t*	*P*	Est.
Intercept	1	16.4	<0.001	0.51 ± 0.031	13.5	<0.001	1.0 ± 0.12
Group size	1	−5.0	<0.001	−0.016 ± 0.003	6.0	<0.001	0.047 ± 0.008
Habitat stubble	1	−1.0	0.18	−0.023 ± 0.023	−1.5	0.13	0.001 ± 0.056
Distance to road 100–300 m	2	−4.6	<0.001	−0.11 ± 0.024	−1.1	0.27	−0.089 ± 0.058
Distance to road >300 m		−3.8	<0.001	−0.10 ± 0.027	0.02	0.98	−0.073 ± 0.065

Data for proportion of individuals scanning were reasonably normally distributed and the distribution of the residuals from final models did not violate assumptions on visual inspection (Crawley 2007). Group scan frequency was not normally distributed and so the data were arcsine transformed so that the distribution of the residuals from final models did not violate assumptions (Crawley 2007). We used a General Linear Model (GLM) including habitat and distance to road as fixed factors, and group size as a covariate to test the effect of group size, habitat and distance to road on vigilance behaviour (Li & Jiang 2008), and to analyse the source of any variance (i.e. the main contributory factors) in vigilance (Mazer 1989). Statistical analyses were done with the SPSS19.0 and using R (version 3.0.1; R Core Team 2013). Significance levels were set at 0.05.

Overall, our results indicated that the percentage of individuals scanning in a group was smaller in bigger flocks but the total vigilance level of a flock increased with group size. The percentage of individuals observed scanning during a session was on average 32.0% and ranged from 8.6% to 66.7%. There was a clear decrease in proportion of individuals scanning in a group with group size (Table 1, Fig. 1) and with distance to road (Table 1 and Fig. 1). There was no strong evidence for an interaction between group size and distance to road ($F = 1.0$, $P = 0.38$, interaction added into the model in Table 1), although the percentage of individuals scanning greater than 100 m were very similar suggesting that the effects of roads on vigilance act on a scale of less than 100 m (Fig. 1). Great Bustards had the same vigilance level in different habitats (Table 1). Group size accounted for 17.7% of the variance at the group scan level, 13% by distance to road and 2.9% by habitat. The average group scan frequency was equal to 86.3% and ranged from 33.3% to 100% (Fig. 2). There was a clear increase in the proportion of time at least one bird was vigilant with group size (Table 1, Fig. 2) but not with distance to road or habitat (Table 1). The interaction between group size and distance to road was not significant ($F = 0.04$, $P = 0.96$, interaction added into the model in Table 1). Group size accounted for 32.7% of the variance in the group scan frequency, 2.2% by habitat and 1.9% by distance to road.

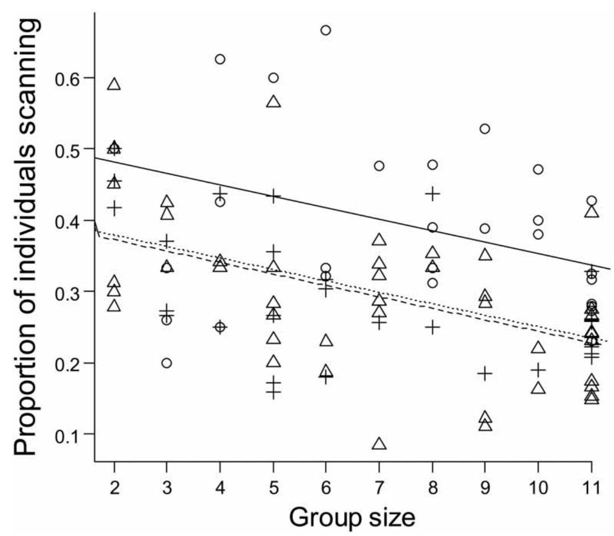

Figure 1. The relationship between individual group scan level (proportion of individuals within the group that were engaged in scanning during a session) and group size and how this varied with distance to the road. The solid line is the predicted line from the model in Table 1 for winter wheat fields and at distances to road of <100 m (circles). The dashed lines are for distances 100–300 m (triangles) and >300 m (crosses) to the road and their intercepts are not statistically different but both are statistically different from the <100 m line (Table 1).

Our results demonstrated that group size had a significant effect on the vigilance behaviour of Great Bustards at both the individual scan level and the overall group scan frequency. The scramble competition

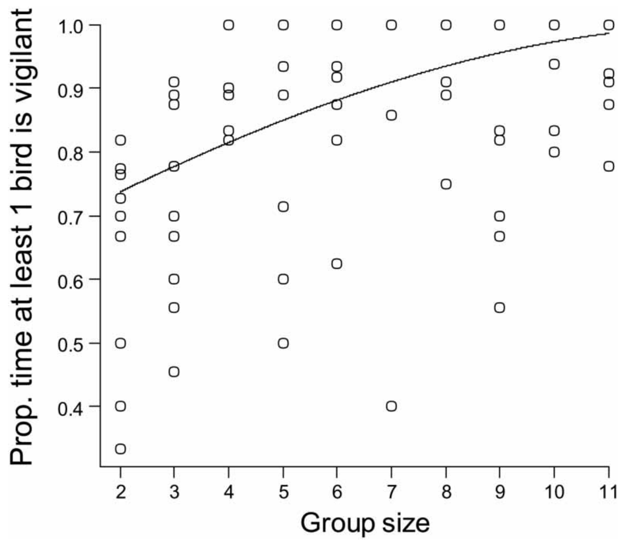

Figure 2. The relationship between group scan frequency (proportion of time that at least one bird of the group was vigilant) and group size. The solid line is the predicted line from the model in Table 1 (back transformed) for winter wheat fields and at distances to road of 100–300 m.

hypothesis could explain this phenomenon where food resources are limited and an increasing number of foragers compete to obtain a diminishing share of resources at the expense of vigilance (Beachamp & Ruxton 2003), however we believe that competition for food was in fact low, due to the overall low density of birds over the study area. As a consequence, we consider that predation effects (the detection hypothesis and dilution hypothesis) were most likely to be the most important factors affecting the group size effect on vigilance in Great Bustards. However in Spain, a correlation between group size and vigilance in the Great Bustard was not found, and only solitary individuals spent more time on vigilance (Martínez 2000).

Although individual scan levels decreased in larger groups, collective vigilance increased. Overall group scan frequency (collective vigilance) in Great Bustards was on average 86.3% and it remained unchanged with respect to disturbance distance from the road. Therefore, Great Bustards likely maintain a high level of vigilance against potential predators even when undisturbed as long as they are in large groups. This has also been demonstrated in many animal species, such as Ostriches *Struthio camelus*, ground squirrels *Xerus inauris* and Degus *Octodon degus* (Bertram 1980, Ebensperger *et al.* 2006, Edwards & Warterman 2011, respectively). Feeding birds are dependent on the vigilance of other members of the group, because alert individuals respond to attack more quickly (Elgar *et al.* 1984, Lima 1995). Such high levels of vigilance can probably ensure the Great Bustard groups spot possible danger whatever the level of disturbance, but not at the expense of increasing vigilance time of each individual – individuals can lower their investment in vigilance while still benefiting from efficient group vigilance (McNamara & Houston, 1992).

We also found that individual scan levels increased when the Great Bustards were near the road (<100 m to the road), which in our study area may have represented an area of higher perceived predation risk. Increased predation threats lead to higher individual vigilance levels in many species (Caraco *et al.* 1980, Saino 1994, Ward *et al.* 2000), and birds usually react to human disturbance in a similar way as to predation risk (Frid & Dill 2002). Several studies have shown that human-induced disturbances can have a significant effect on vigilance behaviour (Wang *et al.* 2011), energy budgets (Riddington *et al.* 1996), foraging efficiency (Burger & Gochfeld 1991) and breeding success (Parsons & Burger 1982). Reducing the number of roads in Great Bustard habitat is, therefore, likely to be important to allow birds to decrease their investment in vigilance and so potentially to increase their feeding time. This may be particularly important for populations that are fuelling for migration.

In conclusion, we found that the group size of the Great Bustard had a negative effect on individual group scan levels and a positive effect on the group scan frequency (collective vigilance). Moreover, human disturbance, as a possible perceived predation risk, led to higher individual vigilance levels. Therefore, the implications for conservation of the Great Bustard are to maintain continuous areas of high-quality, undisturbed habitat where they can survive in high enough density to form large groups: this will likely increase Great Bustards' investment in feeding time and as a consequence, increase their survival.

ACKNOWLEDGEMENTS

Many thanks to Prof. Will Cresswell and two anonymous reviewers to enhancing previous versions of the manuscript. We thank Patricia Johnston for editing our manuscript and Yong Zhang for providing logistic support during the fieldwork period.

FUNDING

This work was supported by the West Light Foundation of the Chinese Academy of Sciences [grant number XBBS201308]; the National Natural Science Foundation of China [grant number 31401988], [grant number U1303301]; the Chinese Academy of Sciences Visiting Professorships for Senior International Scientists Program [grant number 2011T1Z42].

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(MS received 21 January 2015; revised MS accepted 30 April 2015)