Red deer *Cervus elaphus* blink more in larger groups

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ABSTRACT

Most animals need to spend time being vigilant for predators, at the expense of other activities such as foraging. Group-living animals can benefit from the shared vigilance effort of other group members, with individuals reducing personal vigilance effort as group size increases. Behaviours like active scanning or head lifting are usually used to quantify vigilance, but may not be accurate measures as the individual could be conducting them for other purposes. We suggest that measuring an animal's blinking rate gives a meaningful measure of vigilance: increased blinking implies reduced vigilance, as the animal cannot detect predators when its eyes are closed. We demonstrate that as group size increases in red deer, individuals increase their blink rate, confirming the prediction that vigilance should decrease. Blinking is a simple non-invasive measure, and offers a useful metric for assessing the welfare of animals experiencing an increase in perceived predation risk or other stressors.

INTRODUCTION

Most animal species spend some part of their lives aggregated together in groups, and many benefits have been proposed and tested for this behaviour [1,2]. For prey species, grouping behaviour can offer protection from predators through both the dilution of individual risk if an attack occurs [3–5] and an increase in the chance of successfully detecting an approaching predator due to the combined vigilance effort of the group [5–7]. If an animal is being actively vigilant, it may be unable to conduct other important behaviours (like foraging or resting) at the same time as the vigilance behaviour. Group membership means that vigilance can be pooled among the group members, which could mean that each individual can spend less time being vigilant and more time conducting other fitness-enhancing behaviours. A rich body of theory and research has explored how group size and individual vigilance effort are related [8–11], with much of it focussing on the prediction that individual vigilance effort will decrease as the group becomes larger. This prediction requires each individual to show a trade-off between vigilance and other behaviours, where being actively vigilant either cannot occur at the same time as other behaviours, or leads to a reduction in the efficiency of other behaviours that are conducted at the same time as being vigilant.

Vigilance is usually assumed to be occurring when an animal is actively scanning its surrounding environment with its head upwards, although there is no obvious consensus in how vigilance is defined in any particular species (see [12] for discussion of this problem in studies on primates). Although scanning behaviour is likely to stop an animal from actively collecting food, this head-up activity may not completely interfere with simultaneous conducted behaviours, such as chewing or social interaction. If a behaviour that is recorded as vigilance allows an individual to do other things at the same time, then we may be falsely assuming that this behaviour incurs the time and attention costs that are associated with vigilance [13]. Without careful experimentation, it is difficult to assess how much of an individual's attention is devoted to vigilance when we observe scanning or other forms of vigilance-like behaviour, which may add to the huge variation (*e.g.* [8]) in whether a study demonstrates that individual vigilance is related to group size or not.

Although it is difficult to define exactly when an individual is being vigilant, we may instead be able to define when it is *not* able to be vigilant. Blinking (the temporary closure of both eyes, involving movements of the upper and lower eyelids [14]) is a good example of an activity where an individual is momentarily unable to visually scan the environment. It is an

essential maintenance behaviour to keep the eyes moist and clean [15], and is conducted tens of times every minute in some species of diurnal mammals [16,17] and birds [18]. This frequency means that although a blink takes only a fraction of a second, the sum of this loss of visual information could be substantial for the individual. In humans, spontaneous blinking is accompanied by attentional suppression, where the individual experiences a blackout in visual attention for the duration of the blink, meaning that there is no awareness of the temporary blindness and lack of visual information whilst the blinking is occurring [19,20]. Blinking suppresses activity in both the visual cortex and other areas of the brain that are associated with awareness of environmental change [21]. If we assume that other animals show similar attentional suppression, then they are essentially blind and unaware of changes in their visual environment during each blink, which in turn means that they cannot be vigilant for predators.

An individual's blink rate therefore presents a trade-off between the physiological benefits of blinking and the loss of visual information during the blink [15]. If an animal needs to dedicate more time to vigilance in a risky environment, then it has to reduce or suppress blinking to accommodate this increased vigilance. This is anecdotally demonstrated in American crows *Corvus brachyrhynchos*, which reduce their blink rates when looking at potentially dangerous stimuli [22], and in horses *Equus caballus*, which decrease their spontaneous blink rate in response to stress-inducing stimuli [23]. This link between blink rate and vigilance implies that blink rate will also be related to group size. As group size increases, theory predicts that individual vigilance can be reduced [5], and so any requirement to suppress blinking will be relaxed. Blink rate may therefore increase with an increase in group size. Evidence supporting this prediction is anecdotal: a comparison of chickens *Gallus gallus* feeding solitarily or in pairs showed a non-significant increase in blink rate in the group-feeding birds [24], while a comparison of the blink rates of olive baboons *Papio anubis* showed individuals in a small group blinked less than those in a large group (although the two groups were studied in different years). Here, we test this hypothesis by observing the blink rate in a herd of red deer *Cervus elaphus*. Red deer are a prey species that spend most of their lives in dispersed groups, and females have previously been shown to reduce their vigilance behaviour as group size increases [25,26]. Because they show an increase in vigilance in smaller groups, we would therefore predict that they should also reduce their blink rate to avoid losing visual information about their environment.

METHODS

Study area, time and subjects

This observational study was conducted on the herd of red deer within the 40.5 hectare deer park in Ashton Court Estate, Bristol, England (51.4440° N, 2.6378° W), which is composed mainly of open grassland, with scattered forestry and a small area of water. The herd is managed by the Bristol City Council and consisted of c. 110 individuals of varying age and sex. The enclosure is open to the public outside of the rutting season, so the deer are habituated to both dogs and humans. Our observations were conducted during the red deer rutting season; therefore, observations were restricted between 1200 and 1630 h so they were outside of the dawn and dusk peaks of regular rutting activity [27].

Behavioural sampling and observations

A random individual was selected as carried out in previous research on this herd [28]. A random number was drawn between 1-99, with the focal deer being selected by counting linearly from leftmost or rightmost visible deer (the direction was determined by a coin toss). If the random number was higher than the number of visible deer, it was discarded, and the process started again. The selected individual was observed and dichotomously aged (mature or young) and sexed (male or female). The individual was sexed by the presence or absence of antlers, as after one year of age only males have antlers [29]. Age identification was done by the size and morphology of the individual (larger individuals were older). If the individual was observed suckling then its selection was discarded and randomisation was done again; as these young individuals are hard to sex and exhibit behaviours uncommon to the rest of the herd [27]. An estimation of the abundance of each demographic was also recorded, this was done by every individual being aged, sexed and counted on three different days. The average of these demographics was then calculated, and used in the pseudoreplication analyses presented.

Prior to the observations being conducted, the observers were trained in identifying the recorded behaviours. A blink was defined as a rapid full closure of the eye. Group size was defined as the individuals aggregated in no more than five body lengths away from each other. Before starting any set of observations, the observers waited 10 minutes at the site to habituate the deer. All observations were conducted approximately 10-100 m of the focal individuals through a 30× zoom spotting scope (Avian ED82 Magnesium Scope). The

observations for a single selected individual were recorded for a maximum of 10 minutes. At the start of each minute the group size was counted, with blink rate (blinks per minute) being continuously recorded for each minute. If the deer's eye(s) were obstructed or there was a human/animal disturbance the observations were stopped with the current minute's observations being disregarded. A total of 75 observations were collected using this method.

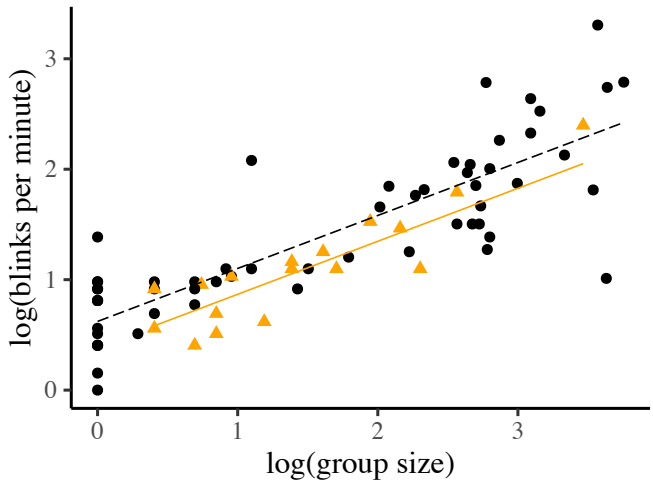
Statistical analysis

Data were recorded as blinks per minute with group size recorded for that minute. Individuals were recorded a mean of 4.9 (± 2.0 SD) minutes before the data collection had to be discontinued due to the observer's view of the eyes being obstructed. For each individual, the mean number of blinks in a minute was calculated, as was the mean group size per minute over the observed period. Analyses described below were conducted using these mean blinks per minute and mean group sizes. To compensate for any unevenness caused by some mean values being based on more observations than others, we conducted the same analyses using just the first minute of data for all individuals (see the Supplementrary Material): these data gave qualitatively similar results to those reported for the analysis involving mean group sizes, and are not discussed further.

All analyses were conducted in *R* 3.6.1 [30]. A linear model was constructed where the natural logarithm of mean blink rate was described by the natural logarithm of group size, and the maturity and sex of the focal individual. Logarithms were used to satisfy model conditions. A full model including interactions was initially considered, but no interaction terms were significant and so the basic additive model with the three explanatory variables was used.

Although attempts were made to avoid replicating observations on the same individual during an observational day, it is likely that the 75 datapoints include some repeat observations of the same individual, given that the herd had 95 observable individuals (of which 11 were estimated to be mature males, 23 were young males, 26 were young females and 37 were mature females), and individuals within each class could not be individually identified accurately. To explore the potential effects of this pseudoreplication on the results, we conducted simulation analyses where identities were randomly allocated to individuals in each age class, and all but one datapoint for each 'assumed individual' was removed from the dataset (code presented in the Supplementary Information). A linear model was then run

172 on this filtered subsample of the dataset, and the significance value was harvested. By
173 conducting 100,000 independent repeats of this resampling, we could identify how likely our
174 dataset was to give a significant result (assuming significance was set at the standard
175 threshold of $p = 0.05$) if we had only sampled each individual once.
176
177
178 **RESULTS**
179
180 We randomly selected individual deer within a herd of c. 110 individuals, and recorded their
181 blink rate over a maximum of ten minutes. At the same time, we recorded the mean size of
182 the local group that they were in, as well as the sex and maturity (young or adult) of the
183 observed individual. A linear model explained the data well ($F_{3,71} = 59.17$, $p < 0.001$,
184 adjusted $r^2 = 0.702$, parameter estimates given in Supplementary Material). Blink rate
185 increased with group size ($F_{1,72} = 172.94$, $p < 0.001$; figure 1), and adults blinked more than
186 young deer ($F_{1,72} = 4.47$, $p = 0.038$; figure 1). There was no relationship between sex and
187 blinking ($F_{1,72} = 0.98$, $p = 0.755$).
188



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191 **Figure 1.** Scatterplot showing that blink rate increases with group size and maturity (where
192 orange triangles and the fitted solid line represent young individuals, and black circles and
193 the fitted dashed line represent adults).
194
195 Considering pseudoreplication of unidentifiable individuals, resampling showed that group
196 size remained significant (at $p < 0.001$) in 100% of simulations. There was a significant (at p
197 < 0.05) effect of sex in only 0.27% of simulations, whilst maturity was significant in 42.97% of

simulations. So, the effect of maturity observed could potentially have been an effect of resampling the same individuals, but the increasing blink rate in response to increasing group size is unlikely to have been affected by any pseudoreplication caused by repeated sampling of the same individual.

DISCUSSION

Our results demonstrate that blinking increases as group size increases. Given that blinking interferes with vigilance behaviour, and that individual vigilance is predicted to decrease as groups get larger, this supports our argument that the blink rate represents a trade-off between gaining visual information through vigilance and the physiological benefits of blinking.

We argued earlier that observed behaviours that are typically recorded as vigilance (such as holding a head upright or active scanning) may not be conducted solely for vigilance. Similarly, blinking may not solely be a maintenance behaviour that is traded-off against being able to collect visual information. Blinking may include a social element, and rhesus macaques *Macaca mulatta* are able entrain their blink rate in response to social cues [31]. However, we suggest that the opposite may be true in red deer: scanning behaviour has been shown to only change in response to group size in females [25,26], but we found that both males and females increased their blink rate as group size increased. In this species, scanning behaviour may be influenced by social behaviour as well as vigilance, but our blinking results may demonstrate that the proportion of scanning time that an individual allocates to vigilance is related to the size of the pooled group effort. Other aspects of social behaviour may also be important for determining blink rates, such as position within the group. Theory predicts that individuals on the outside of the group should be more vigilant than those in the middle, and anecdotal evidence from olive baboons suggests that peripheral individuals may blink less [32]. It may be possible to test many of the standard predictions connecting vigilance and group size (e.g. [8–11]) using blink rate as a proxy for vigilance.

The blink rate may also be influenced by factors other than the size of the group, including rainfall and wind (which have been shown to influence blink rate in captive grackles *Quiscalus mexicanus* [33,34]). Similarly, the behaviour that an individual conducts

simultaneously to the blink may be important. Experiments in humans a mechanism controlling the timing of blinks, which occurs to minimise the chance of missing crucial information [15,35–38], with evidence of similar behaviours in rhesus macaques *Macaca mulatta* [31]. Peafowl *Pavo cristatus* also time their blinks to coincide with gaze shifts [39] while chickens blink more when feeding when compared to scanning [24], both minimising the time where visual information cannot be collected from the environment. Therefore, if an individual is moving, the timing and frequency of its blinks may reflect this movement. Similarly, animals in different attentional states may change their frequency of blinking, such as during sleep in herring gulls *Larus argentatus* [40].

Our results suggest that the measurement of blinking presents a simple and non-invasive technique for observing attention that can be conducted remotely. Although we conducted our sampling in the field, this could be done using video footage. Being able to analyse video footage means that information about blink duration can also be collected, and previous studies have demonstrated that this additional metric, which gives another measure of the length of time when an animal cannot be vigilant, can also vary between individuals and species [17,24,32–34]. Given that blinking has been shown to decrease under stressful conditions [22,23], this simple technique could help us to understand the welfare requirements of managed animals that normally live in social groups.

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AUTHOR CONTRIBUTIONS

ZWR: Conceptualisation, experimental design, data collection, drafting, and editing.
JHR: Conceptualisation, experimental design, data collection, drafting, and editing.
SAR: Conceptualisation, supervision, experimental design, analysis, original draft, and editing.

SUPPLEMENTARY MATERIAL

Two files are included: 'blinkdata.txt' is the raw data analysed, and details the mean blinks per minute, mean group size, sex (f=female, m=male), and age (m=mature adult, y=young) for each datapoint. 'analysis.R' presents the annotated R code used for analysis.

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