Red deer *Cervus elaphus* blink more in larger groups

Zeke W. Rowe*, Joseph H. Robins* and Sean A. Rands†

School of Biological Sciences, University of Bristol, Life Sciences Building, Tyndall Avenue, Bristol BS8 1TQ, United Kingdom

ORCID: ZWR: 0000-0002-9617-5539
JHR: 0000-0001-8980-8150
SAR: 0000-0002-7400-005X

* JR and ZR are considered as joint first authors

† author for correspondence: sean.rands@bristol.ac.uk

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], along with other anti-predator advantages of grouping behaviour such as synchronising activity to dilute risk [8–11]. If an animal is being actively vigilant, it may be unable to conduct (or less efficient at) other important behaviours (like foraging or resting) at the same time (*e.g.* [12]). 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 [13–16], 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 [17] 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 [18]. 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*. [13]) 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 eyelids [19]) 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 [20], and is conducted tens of times every minute in some species of diurnal mammals [21–23] and birds [24]. Although a blink takes only a fraction of a second, the sum of this loss of visual information over multiple blinks 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 [25,26]. Blinking suppresses activity in both the visual cortex and other areas of the brain that are associated with awareness of environmental change [27]. 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 [20]. 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 [28], and in horses *Equus caballus*, which decrease their spontaneous blink rate in response to stress-inducing stimuli [29]. 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 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 [30], while a comparison of the blink rates of olive baboons *Papio anubis* [31] 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 rates of group-living red deer *Cervus elaphus*. Red deer are a prey species that spend most of their lives in dispersed groups, and females are known to reduce vigilance behaviour as group size increases [32,33]. Because they increase vigilance in smaller groups, we therefore predict that they should also reduce their blink rate to avoid losing visual information about their environment. Given that vigilance has been shown to be related to the sex and age of an individual [32,33], we included these individual characteristics in our analysis.

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. The herd, managed by Bristol City Council, consists of *c*. 110 individuals of varying age and sex, who appear to mix freely. 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 over five days during the rutting season; observations were restricted between 1200-1630 h so they were outside of the dawn and dusk peaks of regular rutting activity [34].

Behavioural sampling and observations

A random individual was selected as described in previous research on this herd [35]. The selected individual was observed and dichotomously aged (mature or young) and sexed (male or female). The individual was sexed by the presence of antlers, as after one year of age only males have antlers [36]. Age was identified by an individual's size and morphology (larger individuals were older). If the individual was observed suckling, it was discarded and randomisation was repeated, as young individuals are hard to sex and exhibit behaviours uncommon to the rest of the herd [34]. A count of the total number of young/mature males and females, along with suckling young, was made on three different days. The rounded averages of these five demographic classes were calculated, and used in the pseudoreplication analyses presented (see the Supplementary Information).

Prior to the study, the observers (ZWR and JHR, who both conducted the measurements described) were trained in identifying the recorded behaviours, and pilot trials ensured repeatability of measurements. A blink was defined as a rapid full closure of the eye. Group size was arbitrarily defined as the number of individuals aggregated no more than five body lengths away from at least one member of the group containing the focal deer, meaning a measured group was composed of individuals associated by a chain rule of association (see [37] for discussion of defining groups by associated neighbours within arbitrary distances). Before starting any set of observations, the observers waited 10 minutes at the site to habituate the deer. Observations were conducted approximately 10-100 m away from focal individuals using a 30× zoom spotting scope. An observation for a single selected individual was recorded for a maximum of 10 minutes. At the start of each minute the group size was counted by one observer, with blink rate (blinks per minute) being continuously recorded for each minute by the other observer. If the deer's eye(s) were obstructed or there was a human/animal disturbance the observations were stopped with the current minute's measures being disregarded. 75 individuals were observed 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, we calculated the mean number of blinks in a minute, and the mean group size per minute. 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 Supplementary Material): these data gave qualitatively similar results to the analysis involving mean group sizes, and are not discussed further.

Using *R* 4.0.3 [38], we constructed a linear mixed effects model 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, including the observation date as a random effect. 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. The Supplementary Material describes resampling analysis conducted to explore any effects of pseudoreplication arising from potentially observing the same individuals multiple times.

RESULTS

Blink rate increased with group size (t_{67} = 11.38, p < 0.001; figure 1), and adults blinked more than young deer (t_{67} = 2.11, p = 0.038; figure 1). There was no relationship between sex and blinking (t_{67} = 0.35, p = 0.727). Model estimates and effect sizes are given in the Supplementary Material, along with analyses demonstrating that pseudoreplication is unlikely to have influenced the group size effect.

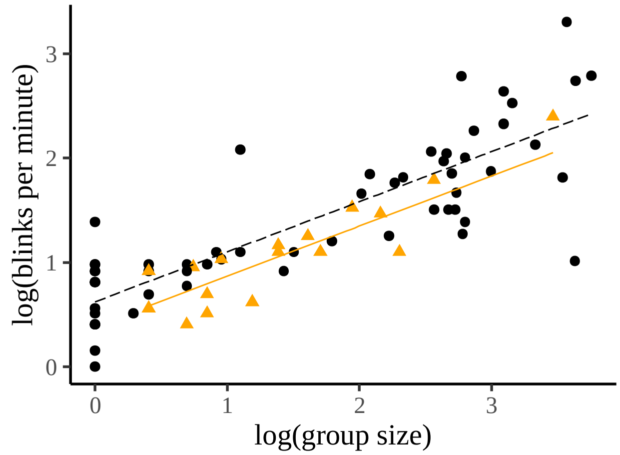

Figure 1. Scatterplot showing that blink rate increases with group size and maturity (where orange triangles and the fitted solid line represent young individuals, and black circles and the fitted dashed line represent adults).

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 note that these results are only correlational, and we suggest that a link between vigilance and blinking could be demonstrated with suitable experimental manipulation of perceived risk (*e.g.* [8,39–41]).

We argued earlier that observed behaviours that are typically recorded as vigilance (such as holding a head upright or active scanning – see [42,43] for discussion) 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, as rhesus macaques *Macaca mulatta* are able entrain their blink rate in response to social cues, coordinating their blinking with partners that they were interacting with [44]. Our results suggest that the proportion of scanning time that an individual red deer allocates to vigilance is related to the size of its immediate group, but we should acknowledge that scanning behaviour may be influenced by social behaviour as well as vigilance. Earlier studies showed that young red deer were less vigilant than older ones [32,33], and suggest this may be because the younger individuals are unlikely to be able to outrun a predator if one appears. If the young in our study are following this behavioural pattern, this also suggests that blinking may not be completely correlated with vigilance level, as the younger deer had low blink rates when compared to mature adults. This may reflect some form of social signalling between adults, although we note that we did not see a difference between males and females (which contradicts previous results showing sex-determined patterns of vigilance, where only females altered behaviour proportionally to group size [32,33]).Other aspects of social behaviour may also be important for determining blink rates, such as position within the group (echoing the vigilance changes seen in [33]). 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 [31]. It may be possible to test many of the standard predictions connecting vigilance and group size (e.g. [13–16]) 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* [45,46]). Similarly, the behaviour that an individual conducts simultaneously to the blink may be important. Experiments in humans suggest a mechanism controlling the timing of blinks, which occurs to minimise the chance of missing crucial information [20,47–50], with evidence of similar behaviours in rhesus macaques *Macaca mulatta* [44]. Peafowl *Pavo cristatus* also time their blinks to coincide with gaze shifts [51] while grackles blink less during flight behaviours [52] and chickens blink more when feeding when compared to scanning [30], all 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, and it may therefore be sensible to assay blinking in response to group size in resting deer groups, which would not be undergoing head and body movements that could confound the measure of blinking that is recorded. Similarly, animals in different attentional states may change their frequency of blinking, such as during sleep in herring gulls *Larus argentatus* [53].

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 can also vary between individuals and species [22,23,30,31,45,46], and may increase in relation to group size [30]. Given that blinking has been shown to decrease under stressful conditions [28,29], this simple technique could help us to understand the welfare requirements of managed animals that normally live in social groups.

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