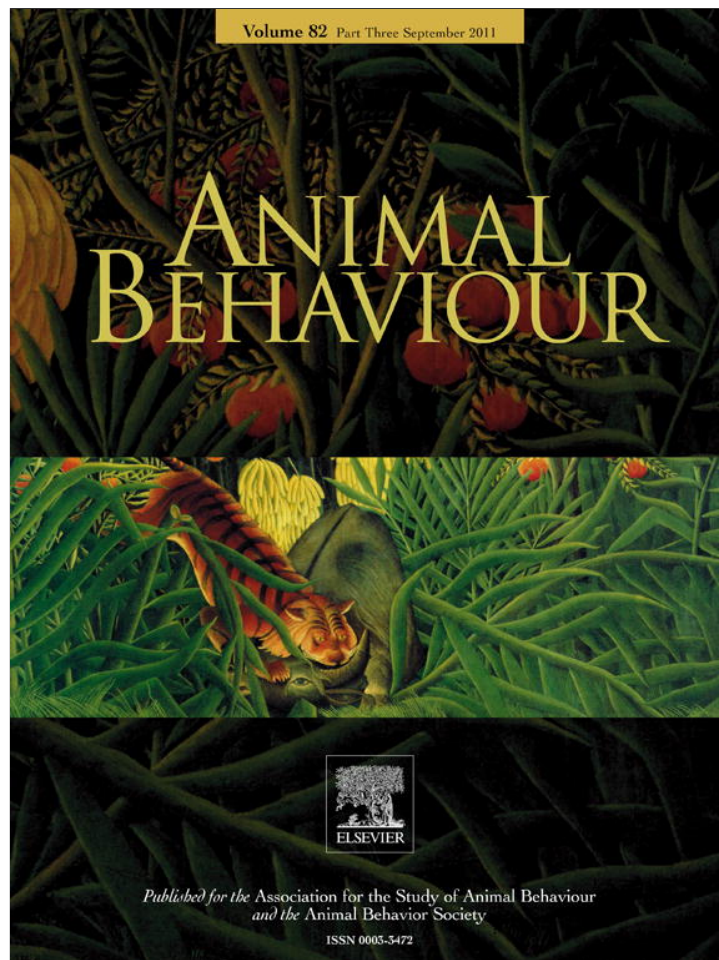


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Making heads turn: association between head movements during vigilance and perceived predation risk in brown-headed cowbird flocks

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Models of antipredator vigilance show that animals should be more vigilant when in smaller groups, when neighbours are farther away, and when they occur at the edge rather than at the centre of a group. However, models fail to specify how animals are expected to look out for threats while actually scanning. We suggest that head movements during scanning may represent a way that animals can control the value of scanning while in groups. Head movements can be used to increase visual coverage (visual search) as well as bring features of the environment to more sensitive parts of the eyes (visual fixation). We conducted a seminatural experiment with brown-headed cowbirds, *Molothrus ater*, in which we manipulated group size and neighbour distance, and recorded vigilance for peripheral and central individuals. During scanning, the rate of head movements by peripheral individuals increased, probably to enhance visual coverage due to their higher perceived risk of predation. However, individuals that were farther apart and in smaller groups used a different scanning strategy by reducing their rate of head movements (e.g. increased the averaged time they spent holding a given head position steady), probably to fixate their gaze longer on neighbours. Visual fixation may be useful for obtaining social information about predation threats from the behaviour of groupmates. We show that (1) a vigilance metric associated with head movement behaviour, which is attuned to the visual system of a species, can provide novel information about vigilance in groups, and that (2) birds have different head movement strategies, probably associated with different visual targets, when the risk of predation is higher.

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Antipredator vigilance (or scanning) allows animals to gather cues in the environment that indicate potential predation threats. There are two classes of cues: direct and indirect. An individual can detect threats directly through its own scanning, or indirectly through monitoring groupmates (Lima 1995). An individual that fails to detect a threat directly can still escape by detecting the reaction of neighbours flushing in response to a predator attack (Hilton et al. 1999). Therefore, investing time in vigilance can reduce predation risk by allowing an earlier detection of predators and more time to escape (Pulliam 1973). Additionally, an individual in a group can benefit from dilution of predation risk when predators target only one individual per attack and when groups are less likely to attract

predators (Foster & Treherne 1981). Collective detection and dilution are two main reasons why individual investment in vigilance is expected to decrease in larger groups (Krause & Ruxton 2002). This group size effect on vigilance has been corroborated empirically in many taxa (e.g. Sullivan 1984; Blumstein et al. 1999; Fairbanks & Dobson 2007; reviewed in: Elgar 1989; Beauchamp 2008).

The relative positioning of individuals in a group is also thought to influence vigilance. Generally, individuals at the centre of a group decrease their investment in antipredator vigilance relative to those at the edge (e.g. Lazarus 1978; Hirsch 2007). Individuals at the edges of groups also often experience more predation (Quinn & Cresswell 2006; Romey et al. 2008). This is because a central individual's domain of danger within a group is much smaller since companions at the edges provide layers of protection against attacks originating from outside of the group (Hamilton 1971). Additionally, antipredator vigilance should increase when foragers in a group are more dispersed (e.g. Proctor et al. 2003; Fernández-Juricic et al. 2004). This prediction arises because collective detection may be less efficient when individuals are farther apart and/or because the protection provided by the presence of groupmates decreases.

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Antipredator vigilance is generally measured as the proportion of time individuals spend with the head raised above the ground (Caro 2005), as the chances of detecting predators tend to be higher in head-up compared to head-down postures (Lima & Bednekoff 1999; Tisdale & Fernández-Juricic 2009). Models predict how much time individuals should allocate to antipredator vigilance (i.e. time with head-up) as a function of group size, group density and spatial position to maximize their survival (Pulliam et al. 1982; McNamara & Houston 1992; Ale & Brown 2007). Nevertheless, these models do not specify what animals should do while scanning in head-up postures. The implicit assumption here is that time spent in a vigilant posture reflects the ability to detect threats. However, the scanning pattern while head-up, which is controlled by how the animal looks out for threats, must matter just as much as the time spent scanning.

Head movements or rapid changes in head orientation while scanning have been noted in many species and have been associated with antipredator vigilance (e.g. Lazarus 1979; Cézilly & Brun 1989; Bekoff 1995; Franklin & Lima 2001; Jones et al. 2007, 2009). Lazarus (1979) recorded a decrease in head movement rate with flock size, consistent with the hypothesis that head movements are sensitive to predation risk, but Lazarus also included time spent searching for food in the calculation, thus mixing up frequency of vigilance bouts and head movement rate during scanning. Cézilly & Brun (1989) reported that the mean duration of a particular type of head movement was shorter in pairs than in solitary birds, but only under a specific type of food distribution, which suggests that part of the adjustment in head movement duration was related to food searching. Bekoff (1995) found that changes in both body position and head position decreased with group size when calculated over vigilant and nonvigilant time. Such pooling across time and behaviours makes it difficult to interpret the results in terms of antipredator vigilance strategies during scanning. More recently, Jones et al. (2007) proposed that the control of head movements while scanning may represent another behavioural dimension to increase the quality of scanning during a vigilance bout.

In this study, we focus on scanning patterns during vigilance in foraging groups, where individuals face different levels of predation risk related to group size, neighbour distance and spatial position, using head movement as a proxy for vigilance behaviour. We stress that measuring head movement behaviour is not an alternative to traditional metrics of vigilance but rather a complement. Head movements can work in at least two different ways: visual search and visual fixation (Andrew & Dharmaretnam 1993; Wallman & Letelier 1993). First, moving the head allows individuals to search different parts of the visual space and provides wider visual coverage to detect threats (Dunlap & Mowrer 1930; Friedman 1975). Enhancing visual search would lead to an increase in head movement rate (Fernández-Juricic et al. 2010). Second, head movements are useful to bring features of the environment to retinal specializations for better visual resolution (e.g. monitoring groupmates or predators), a process called visual fixation (Land 1999). Retinal specializations are areas in which photoreceptors occur at high density (e.g. fovea, area centralis) and provide high visual acuity in the visual field (Meyer 1977; Collin 1999). Enhancing visual fixation would lead to an increase in the duration of the time spent holding the head steady in a given orientation, actually decreasing head movement rate.

A full analysis of vigilance focusing on head movement behaviour while scanning in relation to group size and other ecological factors associated with predation risk remains to be done. The aim of our experiment was to assess whether birds at the centre and edge of a group used different scanning patterns, based on head movement behaviour, in groups of different sizes and different densities. We used the brown-headed cowbird, *Molothrus ater*, as a model system. Given the lateral position of the eyes and the central position of the

retinal specialization in the eyes of cowbirds (Blackwell et al. 2009; Dolan & Fernández-Juricic 2010), we made two alternative predictions about risk perception in groups based on visual search and visual fixation. We predicted that head movement rates would increase and, consequently, that the duration of intervals between head movements would decrease when predation risk was perceived to be higher (edge of the group, smaller group sizes, more distant neighbours). Such an increase in head movement rates would be useful for increasing visual coverage so as to detect potential threats (e.g. predators) more efficiently. Alternatively, when predation risk is higher, individuals may decrease head movement rate (and increase the duration of intervals between head movements) to fix their gaze longer on groupmates and gather visual cues that may facilitate collective detection of threats.

METHODS

Details on the experimental design of the present study have been published previously (Fernández-Juricic et al. 2007; Fernández-Juricic & Beauchamp 2008). In those two studies, we found that vigilance of brown-headed cowbirds was influenced by group size and neighbour distance, based on metrics of vigilance that did not consider head movements: rate and proportion of time in head-up postures. In the present study, we used data from the same experiment but focused our analysis on head movement behaviour.

We conducted this experiment on a grassy area surrounded by black fencing to reduce visual disturbance. We created an artificial flock by placing six enclosures on the edge of a circular arrangement around one central enclosure. Enclosures were made of mesh-wire (diameter 0.60 m, height 0.45 m, opening 0.008 m, percentage open area = 85%) and housed one bird each, which removed physical contact, thus preventing competition for resources, while allowing visual and auditory contact. Each enclosure was laid on a wooden tray containing 5 g of Mazuri® Small Bird Maintenance pellets and 15 g of finch mix (Royal Feeds, Leach Grain and Milling, Co., Downey, CA, U.S.A.). All food items were mixed with a 3 cm layer of sawdust.

All enclosures were always present and their spatial orientation in relation to the focal bird did not change across trials. We formed groups of different sizes (3, 5 and 7 individuals) by manipulating the number of birds present in the experimental arena. We manipulated neighbour distance by varying the distance between the central enclosure and the edge enclosures: close (0 m separation), intermediate (2.5 m separation) and far (5 m separation).

We captured 48 brown-headed adult cowbirds (23 males, 25 females) and chose 14 focal centre birds and 14 focal edge birds (with an equal number of males and females per location in a group). The remaining birds were used to manipulate group size. A given focal edge bird was paired with the same focal centre bird across treatments. Except during trials, birds were housed in indoor cages (0.85 × 0.60 × 0.55 m), with three to four individuals per cage, under a 12:12 h light:dark cycle (lights on at 0700 hours) and ad libitum water and food.

We recorded focal birds at the centre and edge of the artificial flock with two Sony DCR-TRV38 digital video cameras placed 5 m away from the flock. A trial started when the focal bird at the centre pecked. Trials were done in the mornings (0800–1300 hours) for each combination of flock size and neighbour distance (9 treatments, 126 trials). To enhance foraging behaviour, we deprived birds of food during the early morning. We recorded food deprivation time, as trials started at different times during the morning. We kept the sex ratio of individuals surrounding the central focal bird constant across trials.

In this study, we recorded the head movement behaviour of edge and centre focal birds while head-up with JWWatcher 1.0 (Blumstein & Daniel 2007) over 5 min. We specifically recorded the occurrence of

head movement events while focal birds were either stationary or walking. We did not score head movements while animals were flying, hanging from the walls of the enclosure, head-down while searching for food, or pecking or preening. A given head movement began when a cowbird changed the orientation of its head, and finished when the bird's head was in a new stable orientation. Our estimates of head movement occurrences most likely reflected scanning rather than food-searching events, as foraging in this species is performed with the head down. We report only the duration of intervals between head movements (ms) because of its inverse relationship with head movement rate. All videocoding was performed by M.H. (within-observer error <5% after extensive training in recording head movement behaviour in cowbirds in other experiments).

The use of mesh-wire enclosures may have constrained visibility and hence influenced head positioning. However, all individuals were exposed to the same cages across all treatments, reducing the potential confounding effect of enclosure visibility.

Statistical Analysis

We used a repeated measures linear mixed model that included position, flock size, neighbour distance, and their interactions as independent factors. We also added sex and food deprivation time (range 3–7 h) in the models to control for these potentially confounding effects. We used pairwise comparisons (*t* tests) to determine significant differences between levels of each independent variable. Results for the linear mixed model are presented in Table 1, and those for the pairwise comparisons are presented in the text. We log transformed the interval duration between head movements to meet normality of the residuals and homogeneity of variance assumptions, but we report untransformed means \pm SE for clarity. Statistical analyses were conducted with SAS v.9.2 (SAS Institute, Cary, NC, U.S.A.).

RESULTS

The interval between head movements was significantly influenced by position in the group, group size, neighbour distance and sex, but not by food deprivation, and there was no significant interaction between any of these factors (Table 1). Individuals at the centre (389 ± 6 ms) of the group had longer intervals between head movements than those at the edge (369 ± 6 ms; Table 1).

Intervals between head movements were significantly longer in group size 3 than in group size 5 ($t_{52} = 2.62, P = 0.012$) and group size 7 ($t_{52} = 3.01, P = 0.004$), which did not differ significantly ($t_{52} = 0.39, P = 0.697$; Fig. 1a). Intervals between head movements were significantly shorter when neighbours were at close distances than when they were at far ($t_{52} = 3.94, P < 0.001$) and intermediate

Table 1

Effects of position (edge versus centre), group size, neighbour distance, their interactions, and sex and food deprivation time on (log) mean intervals between head movements of brown-headed cowbirds

	<i>F</i>	<i>df</i>	<i>P</i>
Position in group	5.24	1, 25	0.031
Group size	5.37	2, 52	0.008
Neighbour distance	7.83	2, 52	0.001
Position in group*group size	1.06	2, 52	0.353
Position in group*neighbour distance	0.91	2, 52	0.408
Group size*neighbour distance	0.70	4, 92	0.592
Position in group*group size*neighbour distance	0.42	4, 92	0.791
Sex	4.56	1, 25	0.043
Food deprivation time	1.77	1, 195	0.185

Significant values are shown in bold.

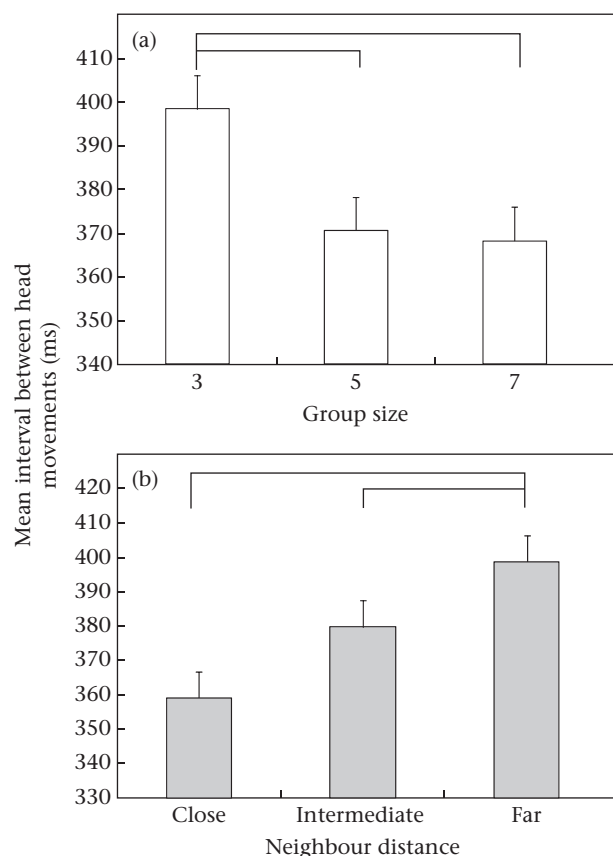


Figure 1. Variations in the mean interval between head movements in relation to (a) group size (3, 5, 7 individuals) and (b) neighbour distance (close = 0 m; intermediate = 2.5 m; far = 5 m) in brown-headed cowbirds. Lines indicate significant pairwise comparisons (see text for details).

($t_{52} = 2.28, P = 0.027$) distances, which did not differ significantly ($t_{52} = 1.62, P = 0.111$; Fig. 1b). Finally, intervals between head movements were significantly longer for males (387 ± 6 ms) than for females (370 ± 6 ms; Table 1).

DISCUSSION

Our investigation of head movement behaviour in the context of vigilance in a group-foraging species revealed distinct scanning patterns. We found that the interval between head movements was shorter in edge birds and longer in all birds when groups were smaller and when groupmates were farther apart. We discuss these results in relation to the results obtained for the same experiment using the traditional metric of vigilance (time spent in head-up scanning postures) from our previous paper (Fernández-Juricic & Beauchamp 2008).

Using head movement behaviour as a metric of vigilance is based on the principle that animals should move their heads from side to side to gather visual information about their surroundings with high visual acuity. Brown-headed cowbirds, as many other ground-foraging species, have wide lateral visual fields with a high density of photoreceptors at the centre of the retina (Blackwell et al. 2009; Dolan & Fernández-Juricic 2010). Consequently, the projection of this retinal specialization towards the right and left sides of the head will determine the spots in visual space that can be seen with the highest visual acuity. This enhanced acuity in the lateral field increases the chances of predator detection relative to that of the binocular field (Devereux et al. 2006). Additionally, head movement

behaviour has been associated with the perception of predation risk as well as the detection and tracking of predators. For instance, Franklin & Lima (2001) showed that solitary birds used head movements to reorient their eyes when facing a visual obstruction to increase visual coverage of the environment. Jones et al. (2007, 2009) found that seed-eating birds adjust their head movement rates before and after detecting a potential predator.

Edge birds experience a larger domain of danger that increases their risk of predation and reduces the benefits of collective detection and dilution. In a previous study in the same system using the time spent head-up versus head-down as a proxy for vigilance (Fernández-Juricic & Beauchamp 2008), we found that individuals at the edge were more vigilant than individuals at the centre. Here, we show that edge birds adjusted their head movement behaviour by decreasing the interval between head movements (i.e. reducing the averaged time that their heads were in a given position). Rapid head movements in edge birds supports the hypothesis that head movements while scanning increase visual coverage of the surroundings with higher visual acuity when predation risk is perceived to be higher (Fernández-Juricic et al. 2010). In other words, getting several snapshots from different parts of the visual space with high acuity can allow edge birds to update the status of their visual surroundings more quickly to check for the presence of threats. In centre birds, in contrast, intervals between head movements were longer, consistent with the idea that head movements of central individuals are used to track other individuals rather than to increase visual coverage quickly (Maldonado et al. 1988; Andrew & Dharmaretnam 1993).

Interestingly, brown-headed cowbirds adopted a different pattern of visual scanning in relation to changes in predation risk brought about by variation in group size and neighbour distance. Irrespective of position in the group, individuals increased the interval between head movements, thus holding the head steady longer, when groups were smaller and when companions were farther away. However, the pattern of change in head movement behaviour was more pronounced in the smallest group sizes and when neighbours were farthest away. One possibility for these results is that the plateaus represent baseline head movement rates when cowbirds are in normal social conditions (e.g. average group sizes and neighbour distances), but as these conditions change, individuals may vary their head movement behaviour to adjust the gathering of social information. This interpretation assumes that individuals in groups that are smaller and more dispersed face higher predation risk, which has been corroborated by previous studies in the same system using the time spent head-up versus head-down as a proxy for vigilance (Fernández-Juricic et al. 2007; Fernández-Juricic & Beauchamp 2008).

The longer intervals between head movements suggest that individuals in smaller and less dense groups were fixating their gaze longer on specific features of their surroundings (Dawkins & Woodington 2000; Moinard et al. 2005). While we do not know exactly what the birds were staring at, we suspect that individuals were fixating on their groupmates to monitor their behaviour. This hypothesis is bolstered by findings from a study on European starlings, *Sturnus vulgaris*, in which more dispersed individuals spent more time orienting their head towards groupmates (Fernández-Juricic et al. 2004). Therefore, under conditions of higher perceived risk of predation brought about by changes in group size and density, brown-headed cowbirds may gather more visual information from groupmates. This can certainly increase the benefits of collective detection in case neighbours detect a threat by quickly detecting variations in their behaviour (Bekoff 1995; Hilton et al. 1999). Alternatively, individuals may monitor flockmates as potential sources of aggressive interactions, which are common in cowbird foraging groups (Morgan & Fernández-Juricic 2007). However, birds in our experiment could not physically interact with each other.

We found that head movement rates of females were faster than those of males. This result was unexpected given that all males and females received the same treatments. One possibility is that there are intrinsic variations in the sensory systems of males and females. For instance, based on preliminary information, the density of photoreceptors thought to be associated with motion detection (e.g. double cones: von Campenhausen & Kirschfeld 1998; Goldsmith & Butler 2005) at the centre of the retina seems lower in female cowbirds than in male cowbirds (A. Ojeda & E. Fernández-Juricic, unpublished data). Consequently, females may be warier of their surroundings than males. Alternatively, males may spend more time monitoring the behaviour of other individuals in their group (e.g. potential mates) than females do. This sex difference certainly merits further research.

We assumed that visual search would lead to an increase in head movement rate and that visual fixation would lead to a decrease in head movement rate, based on previous studies (Andrew & Dharmaretnam 1993; Wallman & Letelier 1993). However, this difference in head movement rate during visual search and fixation may not necessarily be the case in all species. For instance, visual fixation in some bird species may require individuals to switch back and forth from the right to the left eye (Dawkins 2002), as the relative density of different types of photoreceptors may differ between eyes (Hart et al. 2000). Alternatively, visual fixation may require individuals to fixate by aligning different parts of one retina on an object, given the variation in the density of photoreceptors involved in different visual tasks (e.g. colour vision, motion detection, etc.) across the retina (Hart 2001). Therefore, our predictions may not hold for all species and may need to be adjusted depending on the precise visual system of each species.

Our study illustrates how a metric associated with head movement behaviour, which is attuned to the visual system of our model species, can provide novel information about vigilance relative to metrics based on head posture alone, as shown by Jones et al. (2007). Given that information about predation risk can be obtained either directly through individual scanning, or indirectly through monitoring of neighbours, we could not make mutually exclusive predictions about which pattern of head movement should prevail as the level of predation risk varied in the experiment. Additionally, patterns of visual fixation are likely to be interspersed with visual search, as animals may explore certain features of the environment briefly before continuing to search for other objects of interest. A challenge for future research will be to better understand visual fixation in relation to the configuration of the visual system and to develop predictive models that prescribe which scanning pattern should be more prevalent depending on the level of predation risk and the social environment experienced by group foragers.

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