



Social birds copy each other's lateral scans while monitoring group mates with low-acuity vision



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Copying others can be used to enhance foraging and mating opportunities, but can be costly due to the need to monitor the actions of others, which can take time away from foraging and antipredator vigilance. However, little is known about the way animals monitor conspecifics. We investigated the mechanism that European starlings, *Sturnus vulgaris*, use to visually monitor group mates in perching situations through two questions. First, do starlings copy the timing of each other's vigilance? Second, do they use their centres of acute vision to monitor group mates? We studied a component of vigilance that has received relatively little attention, lateral scans, which consist of changes in the orientation of the head (i.e. gaze shifting) while in a head-up position. We found that starlings copied the timing of their neighbour's scans, placing them closer together in time than expected by chance. This could enhance the speed of social information spread within a group compared to random timing of head movements. The strength of this copying effect varied with neighbour distance and the sex of the follower and leader, suggesting that starlings appear to be more motivated to copy some individuals over others. Additionally, instead of monitoring neighbours with their centres of acute vision (high-quality vision), starlings tended to use their retinal periphery (low-acuity vision), potentially reducing the costs of social monitoring. Copying the timing of lateral scans may have advantages for gathering social information (i.e. quick responses to movements of group mates in situations such as murmurations). However, it can also have costs in terms of delaying the detection of personal information by any group member (e.g. predator attack) due to longer gaps without changes in gaze orientation. Therefore, copying the timing of lateral scans may be restricted to specific contexts (e.g. low predation risk).

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Copying consists of imitating the actions of others. Copying can facilitate many fitness-related activities, such as choosing a mate (Losey, Stanton, Telecky, Tyler, & Zoology 691 Graduate Seminar Class, 1986), exploiting novel resources (Boogert, Nightingale, Hoppitt, & Laland, 2014), promoting appropriate levels of vigilance (Lipetz & Bekoff, 1982) and generating collective behaviours (Hemelrijk, van Zuidam, & Hildenbrandt, 2015). Copying can take on many modalities. Animals can copy behaviours (i.e. song: Slater & Ince, 1979; motion patterns: Hemelrijk et al., 2015; feeding behaviours: Dindo, Stoinski, & Whiten, 2011), spatial locations (i.e. local enhancement: Poyso, 1992; joint attention: Emery, 2000), or the timing of activities (e.g. vigilance versus sleeping: Beauchamp, 2011). Ecologically, copying can promote the formation of localized culture, such as dialects in songbirds (Slater & Ince, 1979) or novel

feeding behaviours in primates (Dindo et al., 2011). These localized changes in behaviour can eventually lead to niche separation and speciation (Freeberg, 2000).

One of the gaps in our understanding of copying behaviour is the underpinning mechanisms. Copying requires animals to first monitor the behaviour of group mates, which could be costly (i.e. diverting time from other activities such as foraging, antipredator vigilance, etc.; Ward, 1985). There may be mechanisms that facilitate monitoring and allow copying to be less costly. Moreover, there are different ways to copy, some of which may be more beneficial in some situations than in others. Behavioural ecologists have studied copying the timing of vigilance bouts (head-up orientation) in relation to foraging bouts (head-down orientation) (Bednekoff & Lima, 2005; Fernández-Juricic, Siller, & Kacelnik, 2004; Ge, Beauchamp, & Li, 2011; Podgórski et al., 2016). Two strategies have been proposed to copy the timing of vigilance bouts: coordination and synchronization (Ge et al., 2011; Pays, Jarman, Loisel, & Gerard, 2007; Ward, 1985). During coordination, an individual has its head down when its neighbour's head is up, and vice versa. The

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benefit of coordination is that at any point in time, at least one group member is likely to detect a predator when it appears, enhancing escape responses due to earlier detection (Beauchamp, 2015; Bednekoff & Lima, 1998). However, this is at the cost of having fewer individuals gathering information about a particular threat at the same time, which may reduce the accuracy of assessing the direction of a potential predator attack (Bednekoff & Lima, 1998; Ward, 1985). During synchronization, group mates are more likely to be scanning at the same time with their heads up compared to a random strategy (Ge et al., 2011; Lipetz & Bekoff, 1982; Pays et al., 2007). The benefit of synchronization is that group mates can gather information about threat simultaneously, thereby enhancing the accuracy of the direction of a potential predator attack, but at the cost of time intervals with no vigilance.

Although birds spend a lot of time on foraging substrates, perching also occupies a large proportion of many species' daily routines (Feare, 1984) and it is important for the spread of social information (i.e. acquiring novel foraging task solutions, Boogert et al., 2014). While perching, birds do not have to trade-off foraging with vigilance, as they are oriented with the head up and typically engaged in lateral scans (i.e. moving their heads from side to side, Jones, Krebs, & Whittingham, 2007). These lateral scans change the location of the birds' visual attention, allowing them to 'update' their view of the space around them (Land, 1999; Dawkins, 2002). Lateral scans are important for gathering personal information (i.e. information gathered directly from the environment, such as finding food patches or spotting a predator) and social information (i.e. information gathered from the behaviour of others, such as the presence of conspecifics on a food patch or another individual flushing in response to a threat). For example, when cowbirds experience higher predation risk, they increase their lateral scanning rate, increasing the chances of spotting a predator (Fernández-Juricic, Beauchamp, & Bastain, 2007). Additionally, lateral scans in starlings have been shown to aid in the gathering of information about where a group mate was looking (Butler & Fernández-Juricic, 2014).

Copying (or imitating) the timing of a neighbour's lateral scan could occur in two ways, both of which have important consequences for predator detection through social information, and consequently, collective detection. First, an individual can move its heads shortly after the head movement of a group mate (i.e. lateral scans from neighbours would occur closer in time), leading to social information being detected sooner by group members (i.e. shorter information flow times) compared to independent head movement timing. However, this copying strategy could also lead to longer gaps in time when no group members engage in lateral scans (i.e. gaze shifts), potentially delaying the detection of an approaching predator. Second, an individual can delay moving its head after the head movement of a group mate (i.e. lateral scans from neighbours would be more spaced in time), leading to social information being detected more slowly by group members (i.e. longer information flow times) compared to independent head movement timing. However, this would lead to shorter gaps in time when no group member engages in lateral scans (i.e. gaze shifts), potentially decreasing the time to detect an approaching predator. Additionally, copying the timing of lateral scans would allow for new individuals that have just joined the group to adjust their vigilance levels to those of other group members that have been in the same spot for longer and therefore have a more accurate assessment of risk.

The first goal of this study was to characterize the temporal patterns of lateral scans in perching European starlings, *Sturnus vulgaris*. We used European starlings because their visual system has been well characterized (Dolan & Fernández-Juricic, 2010; Martin, 1986; Tyrrell, Butler, & Fernández-Juricic, 2015).

Additionally many studies have found that starlings use social monitoring (Butler & Fernández-Juricic, 2014; Fernández-Juricic et al., 2004; Templeton & Giraldeau, 1995; Vásquez & Kacelnik, 2000). We predicted that starlings would tend to copy the timing of their neighbour's lateral scans due to their tendency to copy and synchronize other behaviours (e.g. head-up versus head-down patterns, foraging effort; Fernández-Juricic et al., 2004). To test this prediction, we used pairs of starlings and designated one bird as the focal ('responder') and the other bird as the nonfocal neighbour ('initiator'). We used pairs of birds rather than larger group sizes because we were interested in the fundamental mechanisms of copying lateral scans and having larger groups would have added multiple sources of social information (e.g. several neighbours in different spatial positions moving their heads simultaneously), making measurements (and inferences) more challenging. We also examined whether copying is influenced by the sex composition of the group. Starlings are polygynous, with females forming groups of two to four individuals that mate exclusively with a single male and exclude other females from their group (Feare, 1984; Henry, Bourguet, Coulon, Aubry, & Hausberger, 2013). Males must compete with each other for access to these female groups (Feare, 1984). Additionally, under limited food resources, females show impaired auditory learning relative to males, and males show decreased flying abilities relative to females (Farrell, Morgan, & MacDougall-Shackleton, 2016; Verspoor, Love, Rowland, Chin, & Williams, 2007).

Our second goal was to investigate the role of the visual system (e.g. use of acute versus peripheral vision) in monitoring group mates. This is relevant in the context of copying because monitoring others is expected to be costly (Ward, 1985), but these costs have been proposed to be lower for some visual sensory configurations (e.g. wide visual fields; Fernández-Juricic et al., 2004). Starlings have laterally placed eyes, with one centre of acute vision (i.e. fovea) in each eye projecting laterally to two different points in space (Fig. 1a). In addition, their centres of acute vision do not project into the binocular field even when the eyes are converged (see Supplementary Fig. S1). The other areas of the retina (i.e. retinal periphery) provide relatively lower visual resolution, projecting into different parts of the visual field (binocular field, front and rear periphery; Fig. 1a). Finally, starlings have a region of the visual field, the blind area, with little or no visual input except when the eyes are diverged (Supplementary Fig. S1b). We addressed this second goal in multiple ways. First, we established the regions of the visual field (i.e. binocular, foveal, peripheral) that starlings use to monitor their neighbours at different neighbour distances. Based on Dawkins's (2002) findings in chickens, we predicted that starlings would use their binocular fields when they were close to conspecifics (Fig. 1a, dark grey region) but would use their foveae when farther away. Since the flow of social information degrades with distance (Fernández-Juricic & Kowalski, 2011), we predicted that birds would respond more slowly to conspecifics that were farther away. We also examined whether body orientation influences patterns of lateral scanning. We predicted that starlings would be quicker to respond to each other when their bodies were in parallel (i.e. bodies oriented in the same direction, Fig. 1b) than when they were antiparallel (i.e. bodies oriented in opposite directions, Fig. 1b) due to the spatial configuration of their visual system. Starlings have foveae that project slightly forward (about 60.5° caudally of the beak; Martin, 1986; Dolan & Fernández-Juricic, 2010), making the alignment of the centre of acute vision of the focal individual relative to the nonfocal individual easier when the two individuals are oriented in parallel as opposed to antiparallel. Finally, we examined whether the part of the visual field (i.e. binocular, foveal, etc.) used by the focal individual to monitor its neighbour would influence the focal's behavioural

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