1 TITLE: Social birds copy each other's lateral scans while monitoring group mates with low
2 acuity vision

3
4 ABSTRACT

5 Copying others can be used to enhance foraging and mating opportunities, but can be costly due
6 to the need to monitor the actions of others, which can take time away from foraging and
7 antipredator vigilance. However, little is known about the way animals monitor conspecifics. We
8 investigated the mechanism that European starlings (*Sturnus vulgaris*) use to visually monitor
9 group mates in perching situations through two questions. First, do starlings copy the timing of
10 each other's vigilance? Second, do they use their centers of acute vision to monitor group mates?
11 We studied a component of vigilance that has received relatively little attention, lateral scans,
12 which consists of changes in the position of the head (i.e., gaze shifting) while head-up. We
13 found that starlings do copy the timing of neighbor's scans, placing them closer together in time
14 than expected by chance. This could enhance the speed of social information spread within a
15 group compared to random timing of head movements. The strength of this copying effect varied
16 with neighbor distance and the sex of the follower and leader, suggesting that starlings appeared
17 to be more motivated to copy some individuals over others. Additionally, instead of monitoring
18 neighbors with their centers of acute vision (high quality vision), starlings tended to use their
19 retinal periphery (low acuity vision), potentially reducing the costs of social monitoring. Copying
20 the timing of lateral scans may have advantages for gathering social information (i.e., quick
21 responses to movements of group mates in situations such as murmurations). However, it can
22 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).

Introduction

Copying consists of imitating the actions of others. Copying can facilitate many fitness related activities, such as choosing a mate (Losey et al., 1986), exploiting novel resources (Boogert, et al., 2014), promoting appropriate levels of vigilance (Lipetz & Bekoff, 1982), and generating collective behaviors (Hemelrijk et al., 2015). Copying can take on many modalities. Animals can copy *behaviors* (i.e. song (Slater & Ince, 1979), motion patterns (Hemelrijk et al., 2015), feeding behaviors (Dindo, et al., 2011), *spatial* locations (i.e., local enhancement (Poysa, 1992), joint attention (Emery, 2000), or *timing* of activities (e.g., vigilance vs. sleeping (Beauchamp, 2011), etc. Ecologically, copying can promote the formation of localized culture, such as dialects in song birds (Slater & Ince, 1979) or novel feeding behaviors in primates (Dindo et al., 2011). These localized changes in behavior can eventually lead to niche separation and speciation (Freeberg, 2000).

One of the gaps in our understanding of copying behavior is the underpinning mechanisms. Copying requires animals to first monitor the behavior 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. Behavioral ecologists have studied copying the timing of vigilance bouts (body head-up) in relation to foraging bouts (body head-down) (Fernandez-Juricic et al., 2004; Bednekoff & Lima, 2005; Ge et al., 2011; Podgórski et al., 2016). Two

strategies have been proposed to copy the timing of vigilance bouts: coordination and synchronization (Ward, 1985; Pays et al., 2007; Ge et al., 2011). During *coordination*, an individual has its head down when its neighbor's head is up, and visa versa. The 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 (Bednekoff & Lima, 1998; Beauchamp, 2015). 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 (Ward, 1985; Bednekoff & Lima, 1998;). During *synchronization* group mates are more likely to be scanning at the same time with their heads up compared to a random strategy (Lipetz & Bekoff, 1982; Pays et al., 2007; Ge et al., 2011). The benefit of *synchronization* is that since more individuals have their heads up at once, they can all gather information about the threat at the same time enhancing the accuracy of the direction of a potential predator attack, at the cost of leaving longer time periods without anyone being vigilant.

While birds spend a lot of time on foraging substrates, perching does also occupy a large proportion of many species daily routines (Feare et al., 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 between foraging and vigilance as their bodies are head-up and typically engage in lateral scans (i.e., moving their heads side to side, Jones et al., 2007). These lateral scans change the location of their 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 behavior 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 et al., 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 neighbor's lateral scan could occur in two ways, both of which actually have important consequences for predator detection through social cues, and consequently for collective detection. First, an individual can move its heads shortly after the head movement of a group mate (i.e., lateral scans from neighbors 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 member engages 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 neighbors 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 on 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. We used European starlings (*Sturnus vulgaris*) because their visual system has been well-characterized (Martin, 1986; Dolan & Fernández-Juricic, 2010; Tyrrell et al., 2015). Additionally many studies have found that starlings do use social monitoring (Templeton & Giraldeau, 1995; Vasquez & Kacelnik, 2000; Fernández-Juricic et al., 2004; Butler & Fernández-Juricic, 2014). We predicted that starlings would tend to copy the timing of the neighbor lateral scans due to their tendency to copy and synchronize other behaviors (e.g., head-up vs. head-down patterns, foraging effort; Fernandez-Juricic et al., 2004). To test this prediction, we used groups of two starlings and designated one as the focal and the other as a neighbor. We did not use larger groups because this study focused on the fundamental mechanisms of copying lateral scans and having larger groups would add multiple sources of social information (e.g., several neighbors in different spatial positions moving the heads simultaneously), making measurements (and inferences) more challenging. We also asked whether copying was influenced by the sex composition of the group. Starlings are polygynous, with females forming groups of 2-4 individuals that mate exclusively with a single male and exclude other females from their group (Henry et al., 2013; Feare 1984). Males must compete with each other for access to these female groups (Feare 1984). Additionally, under limited food resources, females show more impaired auditory learning and males decreased flying abilities compared to the other sex (Farrell et al., 2016; Verspoor et al., 2007).

Our second goal was to investigate the role of the visual system (e.g., use of acute vs. 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 center of acute vision (i.e., fovea) in each eye projecting into their lateral visual fields to two different points in space (Figure 1a). Additionally, their centers of acute vision do not project into their binocular field even when the eyes are converged (Figure S1). The other areas of the retina (i.e., retinal periphery) provide relatively lower visual resolution, projecting in different parts of the visual field (binocular field, front and rear periphery within the lateral field; Figure 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 (Figure S1b). We addressed this second goal in multiple ways. First, established the regions of the visual field (i.e., binocular, foveal, peripheral) starlings used to monitor their neighbors at different neighbor distances. Based on Dawkins' (2002) findings in chickens, we predicted that starlings would use their binocular fields when close to their conspecifics (Figure 1a, dark grey region), but their foveae when farther away. Since social information flow degrades with distance (Fernández-Juricic & Kowalski, 2011), we predicted that birds would respond more slowly to conspecifics that were further away. We also asked if body orientation influenced 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, Figure 1b) than in antiparallel (i.e., bodies oriented in opposite direction, Figure 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 center of acute vision relative to the non-focal easier when oriented in parallel as opposed to antiparallel. Finally, we asked if the part of the visual field (i.e., binocular, foveal, etc.) used to monitor neighbors influenced the focal's behavioral response using two different measures: (1) latency to respond and (2) the magnitude of the focal's head movement. The

latency to respond can influence the speed with which information flows and the magnitude of a head movement can influence the saliency of cues available to conspecifics (i.e., large head movements may be more salient to neighbors).

Methods

Housing and Capture

We conducted this experiment from November 2014 through February 2015. We obtained the birds in December 2013 using modified decoy traps in Hamilton County, Ohio (N 39.2833, W 84.5947). The state of Ohio does not require a permit to capture European starlings because starlings are an invasive species. There is also no required paperwork to transport European starlings from Ohio to Indiana according to the State and Federal organizations (Ohio Department of Natural Resources: Wildlife; Indiana Department of Natural Resources: Fish and Wildlife; United States Department of Agriculture, APHIS, Wildlife Services). We housed birds in outdoor aviaries (2.5 x 2.5 x 3.5 m) in mixed-sex groups at the Ross Biological Reserve (Tippecanoe County, IN, N 40.4167, W 87.0693) and provided food (cat food and game bird maintenance chow) and water *ad libitum*. Several days before the trials, we moved the birds to indoor enclosures in groups of 2-4 to habituate them to the experimental arena. The Purdue Institutional Animal Care and Use Committee (protocol 1306000876) approved all animal-handling procedures.

Experimental arena and procedures

The experimental arena consisted of a black wire enclosure, approximately 1 m³ in size, with a

UV transmitting Plexiglas top (Loop Acrylics). We placed the enclosure on top of a table covered in brown butcher paper and surrounded the table with black curtains to screen out visual noise and reduce the chances of the focal's head movements being due to external stimuli. We secured a wooden perch 20 cm from the bottom of the enclosure. The birds were able to move along this perch during the experiment. An overhead camera (JVC Everio Full HD) provided a view of the bird heads in most occasions. However, there were several instances where the head was not visible because the animal was at the very edge of the perch, but this happened in less than 1% (85/9,188) of the total head movements recorded, so we excluded these measurements from the analyses.

Based on which birds were present in the indoor housing facility, we arbitrarily chose pairs of individuals for the trials: focal and non-focal (i.e., neighbor). We housed each pair in the same enclosure for at least a day before each trial to familiarize the birds with each other. We tested 23 starlings (13 females, 10 males) as focals. Each bird served as a focal 3 times, and also participated as a non-focal in additional trials. Furthermore, some birds that were never focals participated as non-focals. Each bird only participated (as either focal or non-focal) in a maximum of one trial per day, with at least 2 days between trials. The pairings resulted in 31 opposite sex pairs, 15 female pairs, and 23 male pairs. Birds concurrently participated in another behavioral experiment about visual fixation (where they were exposed to treatments individually), but never within 48 hours of a trial belonging to this experiment. In one trial, the birds never perched together, so we re-ran that trial with the same focal but a different non-focal on a different day.

We food-deprived the animals the evening before trials to standardize their physiological state. Immediately before the trial, we weighed both birds and marked the focal with a dot of

non-toxic paint on the center of its head. Marking birds with paint is common and does not seem to affect the bird's behavior (Burt, 2002). The experimenter (either CH or SRB) placed both birds in the experimental arena and then hid behind the black curtain that surrounded the experimental arena. Each trial lasted 5 minutes, after which the birds were returned to their housing enclosures.

Video coding

We excluded data from the first minute of the trial since the experimenter had just left the arena. If the birds were calm (i.e., flying up < 4 times/minute), we coded the next 2 minute segment of the video, and if not we coded a 2 minute segment later in the video. We included only portions of time when both birds were on the perch and when neither bird was preening.

We coded the trials to assess the focal's response to the head movements of the non-focal using Quicktime (version 7 at 30 fps). We identified all of the head movements of the non-focal that occurred when the focal's head was still rather than moving because visual input is constrained while the head is in motion (Burr et al., 1994; Land, 1999). To exclude the possibility that the head movements of the focal were due to individual vigilance patterns (i.e., independent of the non-focal), we assessed the latency for the focal to turn its head towards or away from the non-focal measured from random points in time as opposed to relative to the non-focal head movements, but still in the presence of the non-focal. We picked 100 random frames per trial and recorded the latency for the focal to move its head after these random frames.

We predicted that if head movements are spaced closer in time than expected by chance, the latency before the focal moved its head after the non-focal moved its head would be significantly shorter than the latency for the focal to move its head after a random frame. On the

other hand, if head movements are more spaced out in time than expected by chance, we predicted that the latency for the focal to make a head movement after the non-focal made one would be significantly greater than after a random frame. Finally, if the timing of the focal head movements is independent of the non-focal head movements (i.e., no copying), the latency for the focal to move its head after the non-focal did would not be significantly different from the latency for the focal to move its head after a random frame.

We specifically chose our sampling method to assign in advance one bird as the non-focal (initiator) and one bird as the focal (responder) for two reasons. First, this sampling approach allowed us to statistically detect the difference between the head movements being closer together or further apart in time. Had we picked an initiator and a responder post-hoc, we would not have been able to statistically detect the difference between the timing of the focal and non-focal head movements. Second, while birds move their heads, visual input is limited (Burr et al., 1994; Land, 1999); thus, we chose to sample only instances when the focal's head was not in motion as the non-focal initiated a head movement because the focal might not have been able to detect it visually. Our sampling approach could double count head movements (i.e., having one head movement of the focal counted as a response to two different head movements of the non-focal, or in response to two random frames), leading to longer latencies in response to the first non-focal head movement. To minimize this bias, we assumed that the response of the focal was to the head movement of the non-focal immediately preceding, and not to any other head movement that occurred before this. Thus, we conditioned the dataset to include only pairs of head movements where the focal was the next bird to move its head after the non-focal. For instance, if the non-focal had made 2 head movements in a row before the focal head moved, we only included the second head movement. Similarly, we excluded random frames that were not

230 followed by a focal head movement before the next random frame.

231   One observer (CH) identified any head movements that were detectable by watching the
232 videos frame-by-frame, where the bird's head was in a different position in two consecutive
233 frames. CH excluded head movements that were up or down (not identifiable as towards or away
234 from the other bird), which happened less than 1% of the time (65/9,188 head movements). CH
235 was 95% consistent with herself in terms of identifying these head movements. We included all
236 head movements that followed the above criteria, even very small ones, meaning that we did not
237 have a "cut off" amplitude. CH also recorded the distance between the birds (in cm), and whether
238 their bodies were oriented in parallel (i.e., in the same direction), or in antiparallel (in the
239 opposite direction) (Figure 1d) relative to each other. Five people coded other aspects of the
240 videos. After SRB engaged in self-training, and once she and the other 4 individuals were all
241 95% consistent with each other in identifying the end of head movements within 2 frames (at 30
242 fps) of each other, they identified the end of all the head movements.

243   We also examined how starlings used their visual system in these interactions. SRB
244 measured the angle of the focal's head relative to the perch at the start and end of each head
245 movement to the nearest degree, using a clear plastic protractor with a string attached. SRB was
246 95% consistent within 2° after self-training. We then projected the location of the non-focal into
247 the focal's visual field. All these calculations were based on published accounts of the European
248 starling retinal configuration (Dolan & Fernández-Juricic, 2010) and visual fields (Martin, 1986).

249   Animals that can move their eyes, like European starlings (Martin, 1986; Tyrrell et al.,
250 2015), have a dynamic visual field: the size of the binocular field, lateral field, and blind area
251 change depending on the eyes being at rest, converged, or diverged (Figure S1). We used this
252 sensory information to divide the focal visual field into 5 categories, while assuming that the

eyes were at rest (Figure 1c): resting binocular field, resting blind area, foveal area, front periphery, and rear periphery. We assigned the resting binocular and resting blind area based on the measurements of the binocular field and blind areas with the eyes at rest (Figure S2). This means that in the area labeled “resting blind area”, starlings can actually gather some visual information when their eyes are diverged (Figure S1). Although we made the assumption that the eyes were at rest, the fovea is a small spot on the retina and using just that projection would correspond to a point rather than a region in the visual field. However, starlings move their eyes (and therefore their fovea) often (Tyrrell et al. 2015) so we defined the foveal area as the sector of the visual field subtended by the fovea between the maximally converged and maximally diverged positions of the eyes (Figure S1). Finally, we assigned the regions in front of and behind the foveal area as the front and rear periphery, respectively. We also used these angles to calculate the magnitude of each of the focal’s head movements by subtracting the final position from the initial angle for each head movement.

Finally, monitoring each other can provide information about the identity (Henry et al., 2013) and sex (Pyle et al., 1997) of an individual. Therefore, we also considered in our statistical analyses the sex of the focal and the non-focal. However, we did not have any a-priori hypothesis about how males and females would respond to group mates.

Statistical analyses

We ran all analyses with SAS version 9.3. We used a generalized linear mixed model whenever the response variable was categorical, frequency or latency, which are not expected to follow normal distributions. We chose link functions based on either predicted distributions when applicable, or whichever distribution or matrix fit best (using -2loglikelihood ratio). For the

analysis involving magnitude, we used a general linear mixed model. All analyses used repeated measures with focal as the subject variable to avoid pseudoreplication. All analyses used the between-within method to calculate the degrees of freedom. We used an alpha value of 0.05 to determine statistical significance.

To assess whether the timing of scans followed either of the two copying patterns (see Introduction) or was independent, we used a generalized linear mixed model, with a log link function and a Poisson error distribution. We used latency of the focal to turn its head after the non-focal head movement as the dependent factor, or a random frame as described above to generate the latency that is expected if the timing of head movements is independent. For our independent factors, we use the event (non-focal head movement or random frame) that preceded the focal's head movement. Our other independent covariates were: sex of the focal (male/female), sex of non-focal (male/female), the interaction between non-focal and focal sex (male focal with male non-focal, female focal with male non-focal, male focal with female non-focal, and female focal with female non-focal), the body orientation of the birds (parallel/antiparallel), and the distance between the birds (continuous, in cm). We used a distance-squared term to check for linearity of the non-focal distance. If starlings were copying the timing of each other's head movements, we would expect a significant main effect of the event preceding the focal head movement (i.e., latency would be significantly shorter or longer after a non-focal head movement compared to a random frame).

We also assessed the relationships between the different independent factors because neighbor distance, body orientation, and sex could be related to each other directly or indirectly. We examined pairs of variables that could have plausible associations between each other (i.e., neighbor distance on body orientation, body orientation on neighbor distance, sex on body

orientation, sex on neighbor distance) in their own mixed model with repeated measures to control for multiple measurements on each focal. We did not examine relationships that had no plausible explanation (i.e., body orientation cannot affect sex). We used a generalized linear mixed model when the dependent variable was latency or categorical, and a general linear mixed model when the dependent variable was continuous. We then calculated the effect size of each pair of variables examined. Additionally, for all independent factors, we estimated the effect size on latency (dependent variable) using Cohen's d with pooled variances both by themselves in their own model (Figure 2). For all other analyses that we ran, we calculated the effect size of each independent factor within the model (while controlling for all other independent factors in model) and their effect sizes are in Tables 1 and 2. When the independent factor had more than 2 levels, we determined the effect size by averaging the absolute value of all of the calculated pairwise effect sizes. To interpret the results, we followed the conventional classifications of effect sizes: effect sizes < 0.2 are considered negligible, effect sizes $\geq 0.2 < 0.5$ are considered small, effect sizes $\geq 0.5 < 0.8$ are considered medium, and effect sizes > 0.8 are considered large.

We also plotted the cumulative distributions of focal latency for head movements following the non-focal and following random frames and performed a two-sample Kolmogorov-Smirnov test to establish whether the pattern of response to the non-focal head movements (copying, random) varied with time since the generalized linear mixed model only provided insights to what happens on average. For the Kolmogorov-Smirnov test, we used bins of a width of 100 ms, allowing us to determine over what length of time if copying differed from chance.

We asked whether the behavioral response of the focal (latency to respond and the magnitude of the head movement) varied with the region of the visual field (right before the beginning of its head movement) the focal was using to monitor the non-focal. To analyze

latency, we used a generalized linear mixed model with a Poisson error distribution, where region of the visual field was the independent factor. To analyze magnitude of the head movement, we used a general linear mixed model with a normal distribution, with the region of the visual field included as the independent factor. For both of these analyses, we controlled statistically for the distance between the birds and sex of both birds and the interaction between the sexes of the focal and non-focal.

We also asked if the region of the visual field that starlings oriented towards the non-focal (right after the end of a head movement) varied with distance. We did this in three steps to ensure that we used appropriate statistical methods but also could interpret our results in a meaningful way. We first tested whether the region of the visual field oriented towards the non-focal varied with distance. We did this by using distance as a continuous independent factor in a generalized linear mixed model with region of visual field (5 categories) as the dependent variable and a multinomial error distribution. This first step (treating distance as continuous) was necessary to ensure that our categorization was not arbitrary. Once we established that distance did influence the region of the visual field used ($F_{1,4954} = 6.19$, $P = 0.013$), we divided distance into three categories (close, intermediate, far) such that each distance had equal sample sizes. We then ran a generalized linear mixed model with multinomial error distribution with region of visual field (5 categories, Figure 4b) as the dependent variable and distance (categorical, 3 levels) as the independent factor, again including focal sex, non-focal sex, and the interaction of these two factors as covariates. We ran pair-wise contrasts to determine specifically which distance categories differed in the distribution of the region of the visual field that was oriented towards the non-focal. To interpret the direction of these relationships, we plotted the raw means of the proportion of scans that ended in each visual field sector.

We also asked whether the latency for the focal to respond was correlated to the magnitude of their head movement. We predicted that short latencies would be correlated with larger magnitudes of head movements because we assumed that both measures result from the same motivational level.

Results

Timing of head movements

The latency for the focal to make a head movement after the non-focal's head movement was significantly influenced by the event preceding the focal head movement (non-focal head movement or random frame) (Table 1a, Figure 2a). More specifically, the average latency was significantly shorter than that predicted by chance (i.e., random) (Table 1a, Figure 2a), suggesting that the focal and non-focal head movements were more closely spaced in time. The sex of the non-focal and the focal influenced significantly the strength of this copying effect, although their interaction was not significant (Table 1a). Female focals responded more quickly to the non-focal, regardless of their sex (Figure 2c). Focals of either sex responded more quickly to male non-focals (Figure 2d). Body orientation, sex of the focal, and sex of the non-focal all had large effect sizes (Table 1a). The interaction between the sex of the focal and the non-focal had a negligible effect size (Table 1a).

The latency between a non-focal's head movement and a focal's head movement was significantly affected by distance, in a non-linear way (Table 1a, linear term: coefficient= 0.01043, squared term: coefficient= -0.00027), resulting in a unimodal, parabolic distribution of latency that peaked (i.e., latency was the longest and hence copying was the weakest) at 19 cm and was lower (i.e., latency was faster and hence copying was more pronounced) on either side

of this peak (Figure 2e). Additionally, body orientation influenced the latency for the focal to respond to the non-focal (Table 1a), with individuals responding sooner when they were oriented in antiparallel positions (i.e., with their bodies oriented in opposite directions relative to each other) compared to parallel (latency least square means: antiparallel = 227 ± 4 ms, parallel = 250 ± 3 ms). Distance and distance squared had negligible effect sizes while body orientation had a large effect size (Table 1a).

Additionally, we found that the copying effect primarily took place over the first 100-500 ms after the non-focal moved its head (Kolmogorov-Smirnov test: critical value $D^*_{23,23}=0.087$, Figure 2f shows these critical values as vertical dotted lines). This means that if an individual is going to copy the timing of the non-focal's head movement, they usually do so within half a second.

We found that sex had large effect sizes on both distance and body orientation (Figure 3). On average, female-female pairs stood furthest from each other (26 ± 1.5 cm) and in parallel most often ($75 \pm 1\%$) compared to other sex compositions, while male-male pairs stood closest to each other (19 ± 1.5 cm) but in parallel less often ($63 \pm 0.9\%$) relative to other sex compositions; and mixed sex pairs fell in between single sex pairs with respect to these two factors (distance: 21 ± 1.5 cm; percent scans in parallel: $67 \pm 0.1\%$). Additionally the effect size of distance on body orientation was negligible, but body orientation had a strong effect size on distance, with birds that stood in parallel standing closer together (21 ± 1.5 cm) than birds in anti-parallel (23 ± 1.5 cm) (Figure 3).

Region of visual field used to monitor the group mate

Figure 4a shows the frequency distributions of lateral scans associated with different

regions of the visual field across different distances, with the grey dotted lines representing the expected frequency distributions if the focal were to use its visual field based on the relative sizes of its different components. We found that the frequency distributions of lateral scans were significantly influenced by non-focal distance (i.e., close, intermediate, far) ($F_{2,36}=9.00$, $P=0.0007$; Figure 4a), suggesting that the region of the visual field that focals tended to orient towards the non-focal varied with distance. More specifically, we found differences between close and far ($F_{1,36}=16.62$, $P=0.0002$), and close and intermediate ($F_{1,36}=7.86$, $P=0.0081$), but not between intermediate and far distances ($F_{1,36}=1.75$, $P=0.194$). The trends suggest that starlings oriented the front portion (binocular field and front periphery) of their visual field towards non-focals at closer distances, but the rear of their heads (blind area and rear periphery) more often when non-focals were further away (Figure 4a).

The region of the visual field that the focal oriented towards the non-focal was influenced significantly by the non-focal sex, the interaction between the focal and non-focal sex, but not by the focal sex (Table 2). The sex of the non-focal had a negligible effect size, but the interaction between the sex of the focal and sex of the non-focal had a large effect size. To interpret these results, we categorized the data in the following way: trials where both individuals were males, both individuals were females, or a mixed sex pair. Figure 4b shows the frequency distributions of lateral scans associated with different regions of the visual field considering the sex composition of the pair, with the grey dotted lines representing the expected frequency distributions if the focal were to use its visual field based on the relative sizes of its different components. We found that the distribution of the regions of visual field was significantly different between all pairwise comparisons (female-female vs. male-male pairs $t_{16}=16.05$, $P<.0001$; female-female vs. mixed sex pairs, $t_{16}=8.15$, $P<.0001$; male-male vs. mixed sex pairs,

$t_{16} = 9.33$, $P.0001$). The focal within female-female pairs tended to orient its binocular field towards the non-focal more than in male-male or mixed sex pairs (Figure 4b). However, the focal in female-female pairs tended to orient its resting blind area towards the non-focal less than the focal involved in male-male pairs, but more than the focal involved in mixed sex pairs (Figure 4b). Overall, focals involved in female-female pairs oriented the front of their visual field towards the non-focal more, while focals in male-male pairs oriented the back of their head towards the non-focal more, and mixed sex pairs tended to be somewhere in between.

We found that the behavioral response of the focal differed in latency and magnitude depending on the sector of visual field the focal had oriented towards the non-focal, after controlling for the effects of non-focal distance and sex (Tables 1b, 3a, Figure 4c,d). Latency was the shortest (i.e., fastest) when the blind area was directed towards the non-focal (Figure 4c). Latency was also shorter for the front periphery than the rear periphery (Figure 4c). Finally, when focals directed their resting blind area towards the non-focals, they made a larger head movement than when any other region of the visual field was oriented towards the non-focal (Table 3a, Figure 3d). The category of visual field had a medium effect size on both latency and magnitude (Table 1b, 3a)

We found that magnitude was negatively correlated with latency, and that this trend was influenced by non-focal distance, distance squared, and the non-focal sex, but not the focal sex or the interaction between the non-focal and focal sex (Table 3b). Focals (regardless of sex) made larger head movements in response to males compared to females. Birds' distance was associated with magnitude in a non-linear way (Table 3b), peaking (i.e. highest magnitude) around 34 cm and being lower when birds were either closer or further away. The effect size of the non-focal sex was large, but the effect sizes of distance and distance squared were negligible.

Discussion

Group mates in social foraging aggregations have been assumed *not* to monitor the vigilance of neighbors because it would take time away from being vigilant or foraging (Beauchamp, 2002; Ward, 1985). However, more recent evidence suggests that birds do monitor each other, particularly in starlings (Fernández-Juricic et al., 2005, Templeton & Giraldeau, 1996), even at the expense of decreased food intake (Vasquez & Kacelnik, 2000). Our study is the first one to show evidence for a potential mechanism to monitor neighbors' behavior in a perching context through lateral scans. More specifically, we found that starlings copied the timing of each other's lateral scans by individuals moving their heads (i.e., shifting gaze) shortly after group mates moved theirs. The strength of this copying effect was most pronounced at close and far neighbor distances, when the responder was a female, and when the initiator was a male. Irrespective of neighbor distance, starlings tended to monitor their group mates with low rather than high acuity vision.

Starlings have previously been found to temporally synchronize their vigilance bouts (i.e., head-up and head-down sequences) with neighbors (Fernández-Juricic & Kacelnik, 2004) and follow each other's gaze (Butler & Fernández-Juricic, 2014). The lateral scan copying strategy we found in the present study could accelerate the flow of *social* information: an individual that copies the timing of group mates gaze shifts would be quicker to detect changes in conspecifics' head movements than if the individual initiates its lateral scans independently of group mates. This could explain previous results showing that starlings are able to respond so quickly to their neighbor's movements in flocks (Hemelrijk et al., 2015), and potentially in

murmurations. Additionally since the timing of head movements is associated with perceived risk (Fernández-Juricic et al., 2011), copying the lateral scans of group mates could help maintain a similar baseline scanning level across the group. Yet this type of copying behavior would lead to longer gaps when no group mate changes the orientation of its gaze, which could delay the detection of personal information (e.g., an approaching predator) by any group member. One possibility is that our finding was influenced by the relatively low predation risk conditions of our experimental set-up, so future studies should test this type of lateral scan copying behavior under situations with different levels of perceived risk.

Neighbor distance significantly influenced the strength of lateral scan copying in a non-linear (inverse-U) fashion. Actually, neighbor distance has previously been proposed to affect the flow of social information in groups non-linearly (Proctor et al., 2003). Empirical studies supported this prediction in vigilance (Rolando et al., 2001) and neighbor detection (Fernandez-Juricic & Kowalski, 2011) contexts. However, in these studies the response appears to level off with distance, but we found an inverted U-shape relationship: starlings copied lateral scanning when neighbor were either close or far away. Visual resolution decreases with distance, which can decrease the probability of detecting social cues (Fernandez-Juricic & Kowalski, 2011). However, after a certain distance, individuals may compensate for the lower resolution by responding more quickly to any group mate movement. The implication is that individuals may weigh the lateral scans from nearby neighbors differently depending on their absolute neighbor distance by using different parts of their visual field. Actually, starlings tended to use their binocular fields more when looking at their neighbor at close and intermediate distances compared to far distances, similar to what Dawkins (2002) found in chickens.

Starlings appeared to be more motivated to copy some individuals over others. First,

females copied their neighbor (whether male or female) more quickly than males, and both sexes copied males more quickly. This could be due to the dominance of males over females in starling mating system (i.e., polygynous; Feare et al., 1984). This relationship between dominance and social information use is also found in dwarf mongooses: they use social information about predators more when the source is a dominant individual compared to a subordinate individual (Kern, et al., 2016). Second, the magnitude of the focal's head movement was negatively correlated with latency to respond. This means that individuals tended either to respond with a large head movement quickly, or take a longer time to respond and have a small head movement. The large head movements were more in response to a male neighbor than to a female neighbor. Third, females tended to orient the front of their head towards their neighbor more when paired with another female, likely because coloration of the beak can provide information about sex, breeding status, and overall health (Navarro et al., 2010; Pyle et al., 1997). On the other hand, males tended to orient the rear of their heads towards their male neighbors possibly to avoid costly aggressive interactions associated with the beak (Nephew et al., 2005).

Starlings have a relatively wide visual coverage, being able to see approximately 296° around their head (Martin, 1986). Within this large field of view, there are small areas with high (i.e., fovea) and low visual acuity (i.e., retinal periphery). We found that instead of monitoring neighbors with the center of acute vision, starlings use retinal areas with lower visual resolution (i.e., retinal periphery). We speculate that although starlings may monitor group mates with their visual periphery, they may only allocate a small amount of attention to them, leading to a low cost strategy (i.e., not taking up the neural resources devoted to the center of acute vision). This would be enough to detect pronounced changes in the neighbors' behavior that do not require high visual resolution (i.e., neighbor changing the lateral scanning strategy abruptly), but

possibly not enough to pick up on more subtle changes. One of the sensory drawbacks of using the visual periphery is the increase in the degree of uncertainty (entropy) of a cue (Dall, et al., 2005). However, animals could compensate behaviorally for this sensory constraint. We found that starlings responded more quickly and with larger amplitudes of head movements when the neighbor was aligned with their resting blind areas (i.e., very edge of the retina with extremely low acuity or no vision at all) towards each other, likely compensating for the lower quality of information. This heightened response to uncertainty could also be interpreted as an orienting response (i.e., orienting the head or body towards the source of a stimulus) (Sokolov et al., 2002). For instance, humans often reorient their head and/or body towards visual stimuli when they appear far from where their centers of acute vision are currently looking (Corneil & Munoz 2014). Overall, our finding is consistent with other ecological conditions in which uncertainty is high, such as in visually obstructed habitats, where starlings become more vigilant (Devereux, et al. 2005).

The region of the visual field used to monitor neighbors can have implications for the spatial arrangement of individuals in a group. If animals were to monitor neighbors with their centers of acute vision, assuming a fronto-lateral projection of the fovea, as is the case with starlings, we would expect that groups would have a circular arrangement with the beaks facing inwards. Actually, Bekoff (1995) found that grosbeaks in a circular arrangement are less vigilant and more responsive to changes in group size than when in a linear arrangement. If animals were to monitor neighbors with their retinal periphery, assuming a retinal configuration similar to starlings, we would expect groups to have a circular arrangement but with the beaks facing outside of the group. However, this arrangement may not be possible in contexts such as daytime or nighttime roosts as they may require a linear arrangement (Feare, 1984). In this linear

arrangement, if animals monitor neighbors with their retinal periphery, individuals would be expected to orient antiparallel to neighbors (i.e., every other bird's beak pointing in one direction). That is exactly what we found: starlings were quicker to react when their bodies were in antiparallel compared to parallel positions. However, we acknowledge that this interpretation is preliminary because our study included only two birds in a perching context, and these implications may certainly change in larger group sizes. Additionally, daytime and nighttime roosts are often more spatially complex, with tree branches in parallel or in different orientations, and thermoregulatory factors (e.g., wind direction and speed) may affect the energetic costs of certain body orientations. These factors may determine whether starlings orient themselves in a way that allows them to monitor certain neighbors but not others.

Based on the effect sizes, sex composition of the pair appeared to be the main driver of spatial positioning with respect to neighbor distance and relative body orientation. Pairs of two females tended to stand further away and in parallel from each other more often, and orient the front of their heads towards each other more, compared to pairs of two males or mixed sex pairs. The implication is that groups of mostly females might be more vulnerable to predators given that they may have the rear of their heads (i.e., blind areas) oriented towards the edges of the group, reducing the chances of detecting predators. Groups of only males, on the other hand, would tend to have their visual fields facing towards the surroundings standing closer together, potentially facilitating the detection of predators at the edges of a group.

Overall, our findings suggest that having a wide visual field may facilitate monitoring neighbors by reducing attention costs. Using areas with low visual resolution (i.e., retinal periphery) to monitor neighbors may free up the centers of acute vision for gathering other forms of information that require higher visual resolution (foraging, predator detection). Additionally,

utilizing the retinal areas with low visual resolution may allow starlings to monitor more group mates simultaneously due to their wide visual fields. Monitoring multiple individuals at once can increase the accuracy of escape decisions, leading to fewer false alarms (Proctor et al., 2001). Using this sensory perspective to understand how animals monitor each other can help us gain novel insights into the spatial distribution of animals within a group, the speed of information flow, and potentially the mechanisms behind collective behavior.

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Figure legends

Figure 1: a) Visual field of a European starling (*Sturnus vulgaris*). Light grey indicates where one eye can see, dark grey where both eyes can see (i.e. the binocular field) and black where neither eye can see (i.e. the blind area). Reproduced from Martin 1986. b) Body orientations when birds are in parallel and antiparallel orientation. c) Division of the visual field of European starlings based on Martin 1986 and Dolan 2010. We divided it into (A) the resting binocular field; (B) front periphery, the region in front of the most converged position of the fovea and the binocular field; (C) foveal area, the sector between the most diverged and converged position of the fovea; (D) rear periphery, the sector behind the most diverged position of the fovea and the blind area; and (E) the blind area.

Figure 2. a) Starlings copy the timing of non-focals head movements, placing them closer together in time than expected by chance. b) Focals responded sooner when their body was oriented antiparallel to the non-focal as opposed to in parallel. c) Focals responded faster when

the non-focal was a male. d) Female focals responded faster to the non-focals than male focals did. e) Neighbor distance is related to latency in a non-linear way. The grand mean of latency over distance was plotted by running the model without any random factors. Grey lines represent the standard error. f) Cumulative distribution of head movements over latency. Statistically significant copying occurred when the latency was between 100-500 ms, as indicated by the dotted lines.

Figure 3. Effect sizes of sex, neighbour distance, event (neighbour head movement or random frame, see text for details), and body orientation on each other. Effect sizes were calculated using Cohen's D. The effect size for distance on latency and distance on body orientation is an average of the effect sizes from the linear and non-linear terms. Effect sizes were calculated using general (for continuous, normal dependent variables) or generalized (for categorical or non-normal dependent variables) with only one independent and one dependent variable. The effect sizes presented in this Figure differ from the effect sizes presented in Tables 1-3 in that the latter ones were calculated with the full models controlling for the other independent factors.

Figure 4. a) Proportion of scans directed towards non-focal at different neighbor distances. White indicates close neighbor distances; grey, intermediate neighbor distances; and black, far neighbor distances. b) Proportion of scans directed towards non-focal when pairs were either male-male, female-female, or male-female. In both a) and b), the grey dotted lines represent the expected frequency distributions of scan if the focal were to use its visual field based on the relative sizes of its different components. c) Starlings responded sooner to head movements when they oriented their blind area towards the non-focal compared to with other regions of their visual

field. d) Starlings made significantly larger head movements when they detected the non-focal's head movement with their blind area compared to other regions of their visual field.

Figure S1. Configuration of the visual field when starling's eyes are converged or diverged, according to Martin (1986). Light grey indicates the projection into the visual field of one eye, dark grey indicates the projection of both eyes (i.e., the resting binocular field), and black indicates the portion of the visual field without visual input (i.e., the resting blind area).

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Figure
Figure 1

Figure 2

Figure 3

Figure 4

a)

Region of visual field monitoring non-focal's head movement

b)

Region of visual field monitoring non-focal's head movement

c)

Region of visual field monitoring non-focal's head movement

d)

Region of visual field monitoring non-focal's head movement