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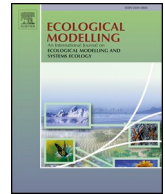
Modelling non-attentional visual information transmission in groups under predation

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ABSTRACT

Group living is of benefit to foraging individuals by improving their survival, through passive risk dilution by sheer numbers and through increasingly more active processes, ranging from cue transmission to alarm calling. Cue transmission of information within a group cannot easily be tracked in the field, but can be studied by modelling. An unintentional visual cue can be given by a fleeing action, and when it occurs in the visual field of an individual, can by contagion incite it to flee as well, making such a cue functional in anti-predator warning. The visual field is limited not only by morphology, causing a blind angle at the back, but also by behaviour. For instance, foraging with the head down can cause an extra "blind" angle in front for cues from other individuals, changing an unobstructed frontal visual field to a split lateral shape.

The questions of the present study are: how do visual fields, in terms of their size and blind angles, influence survival of individuals in a group through their effect on non-attentional reception of cues to danger among group members after attentional detection of a predator, and how can we quantify this?

We use an agent-based spatially explicit model to investigate the effect of contagious fleeing after detection of predators on survival rate. This model is a bottom-up model of foraging agents in a simple environment, where only assumptions about basic competences are made. We vary the size and the shape of the visual field (lateral, with the additional frontal "blind" angle, versus a frontal continuous view), the group size, the movement probability, and the style of movement (regular movement or start-stop movement) in residential groups. We devise a measure for the transmission rate and we measure the length of the transmission chains.

We find that, as expected, in a residential group, a larger visual field enhances survival rate. Moreover, a lateral field is more effective than a frontal field of the same total size because it increases the field of vision and therefore the non-attentional reception of visual cues about danger during, for instance, foraging, for all but the largest visual fields. This is demonstrated by the higher transmission rates and longer chains of transmission for lateral fields. Better transmission for lateral visual fields results in more synchronized fleeing behaviour. As long as the visual field is large enough, having a blind angle in front does not detract from sufficiently effective transmission. These findings should be taken into account in empirical studies of vigilance in groups of foraging animals.

1. Introduction

In nature, living in groups is often described as advantageous when under predation (see for an extensive review Krause & Ruxton, 2002). One of the advantages of living in a group is improved detection of a predator. This arises when individuals transmit information to the other members. In this case, a group functions as a super-organism with "many eyes" (Lima 1995, Pulliam 1973).

However, without information transmission only individual detection is at work; in that case, the probability of detecting a predator is a probability per individual only, and this detection has no effect on others in the group. If there is no transmission, the only benefit of group-living consists of a spreading of risk if a predator can catch only one individual per attack, thereby decreasing the individual risk when more targets are present ("dilution of risk", Bednekoff & Lima, 1998).

Multiplication of the probability of detecting a predator occurs when the animals in a group share information about danger, for instance simply by reacting to visual cues generated by others fleeing (contagious fleeing). If transmission is perfect, one-warned is all-warned, but if the quality of the inter-individual transmission is limited,

this will affect information transfer and therefore reduce survival. Collective detection presupposes perfect transmission (Lima 1995), but that is not guaranteed if cues are visual.

In this paper, transmission depends on the visual perception of individuals. For vertebrates the visual field limitations by morphology range from 210° to 330°, with blind angles at the back (Heesy, 2004, Pita et al. 2016). Foraging group-living animals often have their eyes placed more laterally than predators, giving them a larger visual field, but morphological placement of the eyes does not cause an animal to have a blind angle in front (Martin, 2009, 2017).

Vigilant scanning for predators requires attention, but catching movement cues can also occur in peripheral vision; monocular vision is sufficient to notice other individuals' flight cues. However, frontal "blind" or obstructed angles, in the sense that cues coming in from a distance from other individuals are obscured, can be caused by behaviour, for instance the head-down position when grazing (Lima & Bednekoff 1999a), or being upright but focusing on eating. This behaviour focuses the attention of an individual, but does not preclude non-attentional registering of cues generated by sudden flight in their peripheral vision (see for discussion on peripheral vision for instance Nakayama 1985, Wolfe et al. 2017). Direct detection of a predator could also occur during the non-attentional period, but this seems less probable unless the predator is very close, not least because stealthy movement is less likely to register than sudden fleeing movements (Nakayama 1985).

In groups in nature, it is nearly impossible to separate the individual direct detection of predators from the transmission of information about danger (see Rosenthal et al. 2015 for a discussion). Fortunately, agent-based simulation models can improve insight into the effectiveness of transmission of threat information in a group, also called the Trafalgar effect by Treherne & Foster (1981), after the maritime use of signal flags leading to transmission speed exceeding attack speed. Hence we use a simulation model to investigate the information transmission in a group of individuals. In particular, we investigate how the shape of the visual field (Fig. 2) and limitation on its size influence the intra-group information transmission.

Our model is a bottom-up model of foragers as agents with some embodiment in a simple environment. The assumptions about the competences of the individual are very basic: they have only the pattern recognition needed for living, like finding food and shelter, they are vigilant against predators, and react contagiously to visual cues given out in their environment if these cues occur in their visual field. They do not have any other specific memory or knowledge about other individuals around them (for assumptions used in this model, see the method section).

Predator-prey relations tend to be modelled in mathematical models (Hamilton 1971, Pulliam 1973, Lima & Bednekoff 1999b, Fernández-Juricic et al. 2004, Lehtonen & Jaatinen 2016, Gil et al. 2017, Lecheval et al. 2017); some models include reacting to behaviour of other group members (Sirot 2006, Beauchamp 2016), but there are only few models of animals in small groups where movement in space affects their relative position and therefore the visual sensory information about threats and its cue transmission, such as the models of Van der Post et al. (2013, 2015), by whom this work was inspired. Empirical research about the influence of individual movements and orientations towards one another on cue transmission, has been done for instance by Pays et al. (2013) on vigilance in kangaroos.

For models of much larger groups see for instance Hemelrijk & Hildenbrandt (2012); their model deals with much larger flocks or schools than the present simulation of groups of up to 20 individuals. Communal movement and visual fields have often been modelled: mathematically (Rountree & Sedberry, 2009), in particle models (Newman & Sayama, 2008), in neurobiological models (Lemasson et al., 2009) or in individual-based models (Hemelrijk & Hildenbrandt 2012, Romey & Vidal, 2013). However, these studies do not include agent-based models in connection to cue-motivated predator avoidance, but

focus on continuously incoming information on others' movements, vigilance or feeding.

The aim of this study is to investigate and quantify how visual fields influence reception of the information contained in involuntary visual cues from neighbouring individuals during predator attacks, i.e. without auditory cues or intentional warning signals such as alarm calls.

We study patch-bound residential groups to track how visual information about danger travels through a group. "Residential" is meant here as staying in one patch during one simulated attack. For instance, a patch-bound "residential group" may represent a group of marmots or monkeys moving around within a territory or food patch. Empirical observations on groups have been done on many species, for example: antelopes (Underwood 1982, Hunter & Skinner 1998, Kröschel et al. 2017); baboons (Bettridge & Dunbar 2012); marmots (Blumstein et al. 2001); fiddler crabs (Zeil & Hemmi 2006); meerkats and mongoose (le Roux et al 2009); kangaroos (Favreau et al. 2010, Pays et al. 2013); juncos (Lima & Bednekoff 1999a); ducks (Guillemain et al 2002); starlings and sparrows (Tisdale & Fernández-Juricic 2009); and more general for instance, Krause & Ruxton, 2002.

The model is meant to simulate residential foraging animals, in a (terrestrial) habitat with opportunities, like trees or burrows, to evade predators, using only assumptions that are valid for many species that live in small groups. The reason not to focus on one species is that it is hard not to think of other competences or properties that a species has, like the habit of emitting alarm calls (a signal that is potentially not involuntary), living in a kin group or coordinating their vigilance. That would make it harder to demonstrate more general effects.

In the model, we investigate factors that influence visual transmission by affecting how much information is present, such as group size and size and shape of the visual field for cue reception. We aim to illustrate the benefit of being in a small group and only with simple reaction to cues about danger, a benefit that accrues without attention, and therefore without costs in time, at least in this modelled situation of predator attacks. If false detections occur, higher costs would ensue, but here we focus on transmission during predator attacks, without false detections.

Both dilution and a (modified) "collective detection" are part of this model: dilution causes the individual risk per attack to decline to 5% for an individual in a group of 20, even if individuals do not react to behaviour of others (FoV 0°). "Collective" detection, given a constant vigilance rate, could work not by monitoring others' vigilance, but simply by reacting to others' reactions to danger.

2. Methods

2.1. Model description

The model is a spatial simulation model, based on the work of Van der Post et al. (2013, 2015). Their model explored the advantages of being vigilant over not being vigilant, under the conditions that detection of a predator is distance-dependent and that visual information transmission is perfect. The current model focuses on the effect of the forager's visual field shape and size on the intra-group information transmission, with all foragers being equally vigilant, while using the same distance-dependent detection, in order to investigate the information transmission paths within the group.

We modelled (Fig. 2) a continuous visual field (FoV), called "Frontal" in this paper, and a laterally directed visual field, indicated by the term "Lateral", in which the direct view in front is obstructed by behaviour (like foraging) to cues from other individuals. The visual field shapes are only relevant for intra-group transmission, not for the 360° scans done for predator detection. We included the perfect reception for intra-group cues, as a 360° visual field to measure the maximum transmission, which could also occur if auditory cues were modelled. The range of the visual field was sufficient to include all
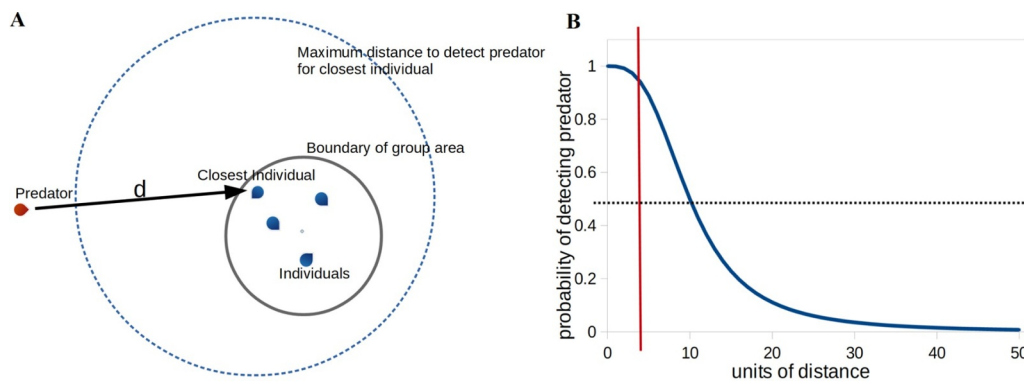
Fig. 1. Principles of the model used in (Van der Post, de Weerd, Verbrugge & Hemelrijk, 2013). A: Spatial set-up of the environment with the predator targeting the closest individual, and location of individuals within the group area defined by a radius adjusted to group size. For the closest individual, the outer circle indicates the maximum distance to detect a predator. B: probability of detecting a predator depends on distance d to that predator. $p = 10^3/(d^3 + 10^3)$, with 50% probability of detection at 10 units of distance (horizontal line). The vertical line represents the capture distance: if the predator is closer, the individual is captured.

individuals in the patch.

We study different group sizes to explore the effects of the amount of information potentially present. The group size influences the amount of information generated and therefore the amount transmitted, and so does the way individuals move (i.e. how they position themselves relative to the others): more detections of predators will lead to more fleeing, more transmission and better survival, as well as less time for other behaviours.

The spatial set-up (Fig. 1) contains a patch-bound residential group, moving within the boundary of a patch or territory. The group area is set to a radius of 10 units of distance for the largest group of 20; the radius is adjusted to group size such that the area per individual is constant, in order to avoid density effects. Our focus is on the individuals in a group, not on the predator. The foragers stay in the same patch, but do not use attention to keep others in sight; indeed it is a purpose of the virtual experiments to define the conditions in which such behaviour is superfluous.

The settings and assumptions used are:

- Small groups of constant sizes, 2-20 individuals, will be attacked by a predator.
- Individuals have only the most basic levels of cognition, which we define as the competence to find food and shelter by pattern recognition mechanisms: individuals are able to detect predators and react to cues generated by others fleeing.
- Individuals stay within a certain distance of each other or within a patch, and have movement probabilities and movement patterns. The predator is initially far away from a group of foragers and targets the closest forager.
- Individuals have probabilities for active scans for predators.
- In the vigilance scan for predators, active attentional scanning is used: the individuals check the whole 360° field, conceptually by head or body turning; this uses both binocular and monocular vision.
- Probability of detection is sigmoidal, with higher probability if the predator is closer.
- A targeted forager must respond to a predator (flee) before the predator is within a critical capture distance from the forager, otherwise the predator attacks and catches the forager while non-targeted foragers escape.
- Individuals flee immediately after detection and this behaviour elicits fleeing unconditionally in others, as long as it occurs within their visual field; cues are noticed because of the suddenness of a change in movement anywhere in vision, whether it is central or peripheral.
- Reception of cues while directing attention to other current activities (like foraging) is non-attentional; this can use both binocular and monocular vision.

The behavioural options of the individuals in the group are shown as a flow chart (Fig. 3).

The exact shape of the sigmoid for the probability density function (Fig. 1, B), introduced and motivated by Van der Post et al. (2013), is not very influential, as long as the probability of detection approaches 1 if the predator is very close, and the probability approaches 0 at the far range of detection. After detection, an individual flees. This fleeing action represents going up into a tree, going down a hole, freezing, or any fleeing behaviour that generates a visual cue, by a sudden change in behaviour or movement. This generated flight cue can be transmitted to others, who react by fleeing contagiously – if they noticed the cue.

The algorithm in the model is as follows: If a scan is performed, and the predator is within maximal visual range, the probability of detection is calculated. If detection follows, the animal flees, generating a (binary) cue. Programmatically the cue generated by the first detection and flight is sent out from the fleeing individual to the others who have not fled yet. They detect a state change, a change in behaviour: If an individual flees (i.e. their behaviour-variable is set to FLEE after detection of a disturbance, or after contagion), all individuals who have that individual in their visual field will be alarmed and will also start to FLEE. The fleeing action takes a time unit, so during this time a predator can still make a kill. After the fleeing action the individual is safe and does not generate cues during the hiding time. To see whether it is safe to come out of its hiding state to resume normal behaviour, a forager scans after 3 time units (during the fourth time unit). If it sees a predator, then it remains in hiding; if it does resume foraging, it becomes a potential target again. However, if the predator is very near at the moment of scanning, the forager is likely to detect the predator and to remain in hiding.

We can measure how strongly the shape of the visual field influences the transfer efficiency of flight cues within the group, because we assume that all individuals are always within the range over which visual cues are noticed; we do not use distance-dependence for intra-group transmission. Having the attention on other behaviour could slow down response (Lima, 1994), but this is partly represented in the model as not receiving the flight cue.

The predator is initiated in a corner of the arena, outside the maximum visual range of any individual. It targets the closest individual and switches targets if this individual flees or if another comes closer. An attack and kill are made if the predator comes within the capture distance of 4 units from its target. This capture distance represents potential changes in predator behaviour, such as acceleration during the actual attack. When all individuals have fled, the predator loses its focus. In order to see how effective intra-group transmission is during an attack, an attack ends in one of these two situations: after maximally one capture; or in the All-Fled condition, when all individuals have fled and thus the predator lost all possible targets. All-Fled indicates success of transmission to all; a capture indicates failure.
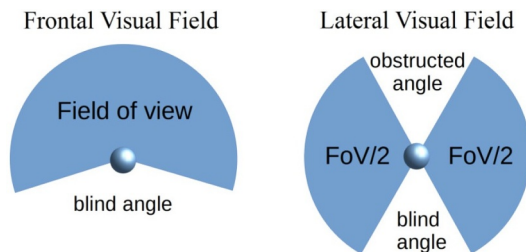
Fig. 2. Shapes of frontal and lateral visual fields for intra-group reception of visual cues. Fields of view (FoV) are shaded, both have the same total size of 240°.

Netlogo™ (Wilensky, 1999) version 6.0 was used for this study, simulating attacks by a predator on a residential group of individuals. Each run simulated one attack; the data were accumulated over 1000 runs, and this was repeated 10 times. All individuals had a vigilance probability rate of 0.1, when scans for a predator were done all around, and had a movement probability rate of 0.1. The individuals had one of the two different field of view (FoV) shapes, lateral or frontal (Fig. 2); group size per run was fixed.

2.2. ODD of the Netlogo™ Model

The simulation model description follows the Overview, Design Concepts, Details protocol (ODD) for describing individual- and agent-based models (Grimm et al. 2006; Grimm et al. 2010). The model is online: https://www.comses.net/codebases/bb167443-5416-4740-8b71-d4a1a818689f/releases/1.0.0/

Purpose. The purpose of this model is to investigate small groups of foragers living under predation and quantify the effects of shapes and sizes of their visual fields on the transmission of information after detection of a predator. Differences in visual fields are caused by morphology combined with behaviour.

Entities and scales. Entities are individuals in an Environment: Foragers who are hunted by Predators.

- Individuals: each individual has an ID, a location, heading and a previous and present action, and moves around in certain movement styles and frequencies. A patch-bound residential group moves around in the middle of the Environment, within a patch defined by the group area radius. The foragers execute their present action, and "decide" on their next action. Behaviours: They can forage, scan for danger, flee, and always react to seeing others flee by fleeing themselves.

- Predator: individual that hunts; it detects foragers that have not fled, and targets the closest visible forager, switching if another gets closer, moves toward this target and kills it if it is within capture distance, or moves along if no forager is visible.

Scales in time and space: Scales are derived from the models of Van der Post et al.(2013, 2015). Time is in the order of seconds to minutes, space in the order of meters. In one time unit, an animal can perform an action such as attentional scanning, which includes head- or body-turning to survey 360°, or move some distance while foraging. Duration of one simulated attack is 300 units. Groups stay within their patch boundary, of which the size is adapted to group size. One simulation run consists of 1000 attacks, with specific settings determining the behaviour of the foragers.

Process overview and scheduling. See Behavioural schema (Fig. 3) and Appendix A.

Design concepts.

Basic principles. Foragers remain with others nearby within a restricted area and exhibit contagious fleeing. i.e. they react to a sudden movement. Low cognition demands: knowledge of others in the group is not needed. The foragers react to perceived fleeing movements of nearby beings, without a concept of "group". The simulated attack stops either at a kill, or when all individuals fled and the predator loses its target; no other interactions.

The model is based on Van der Post (2013), which uses the assumptions discussed previously, except that in their model the automatic detection of a fleeing response is always followed by a fleeing response (perfect detection). The current model uses the same assumptions, while we now add the visual limitations for foragers for detection of that fleeing response.

Emergence. Detection of disturbances and effectiveness of intra-group transmission: the interactions between group sizes and the quality of the transmission of flight cues determine levels of survival.

Sensing. Predators detect any individual not in safety, foragers detect predators visually, and can notice the fleeing action of others.

Stochasticity. Many processes are stochastic: initial location of foragers within the group area, movement, scanning, detection or disturbance.

Observation (see Table 2)

- number of captures per individual and for the group (predator success), and occurrences of perfect transmission (All-Fled);
- how many detections occur within one simulation, and how often contagious flee copying occurs;
- how often no other forager is in view, and how many are in view at the other times;
- length of the transmission chains.
- *Adaptation or learning:* Not present in this model.

Initialization. The parameter settings used for properties like detection distance, speed of approach of the predator, movement frequencies and patterns of the foragers, group sizes and vigilance levels are all based on the model used by Van der Post et al. (2013). At the initialisation, parameters are set for the following characteristics (Table 1) :

- number and duration of attacks, for environment size, group area radius and viewing-ranges,
- for number of predators (1 at a time) and attack distance,
- for forager group size and vigilance level,
- for forager movement types and frequencies,
- and for the shape of the detection probability when actively scanning.

A simulation stops after all individuals have fled (***All-fled***), or after a ***capture***.

Initialization parameters

Sensitivity analysis. Parameter settings for density of the group, range of the visual field for predator detection or for non-attentional cue reception, vigilance, predator speed, kill zone or hiding time were tested to check sensitivity (see Section 3.5 of the results, and Supplementary Appendix G).

Submodels. *Detection.* If a forager is vigilant, the probability p of a forager to detect and respond to a predator declines with distance d to the predator, as follows:

$$P = a\frac{h^n}{(d^N + h^N)}$$

where N determines the slope of decrease in predator detection, depending on distance d to the predator, α sets the maximal detection rate, and h is the distance at which predator detection is half of that maximum. So "distance-dependent production of information" is a key element of the model. Values used in this simulation: $\alpha = 1$, $h = 10$ units, $N = 3$. $\alpha = 1$ insures that detection approaches 100% at very close range.

Transmission. Transmission of the visual cue of another individual fleeing is tested at different qualities: from no transmission at all via limitation by FoV-shape (a frontal or a lateral visual field) and FoV-size to perfect transmission.
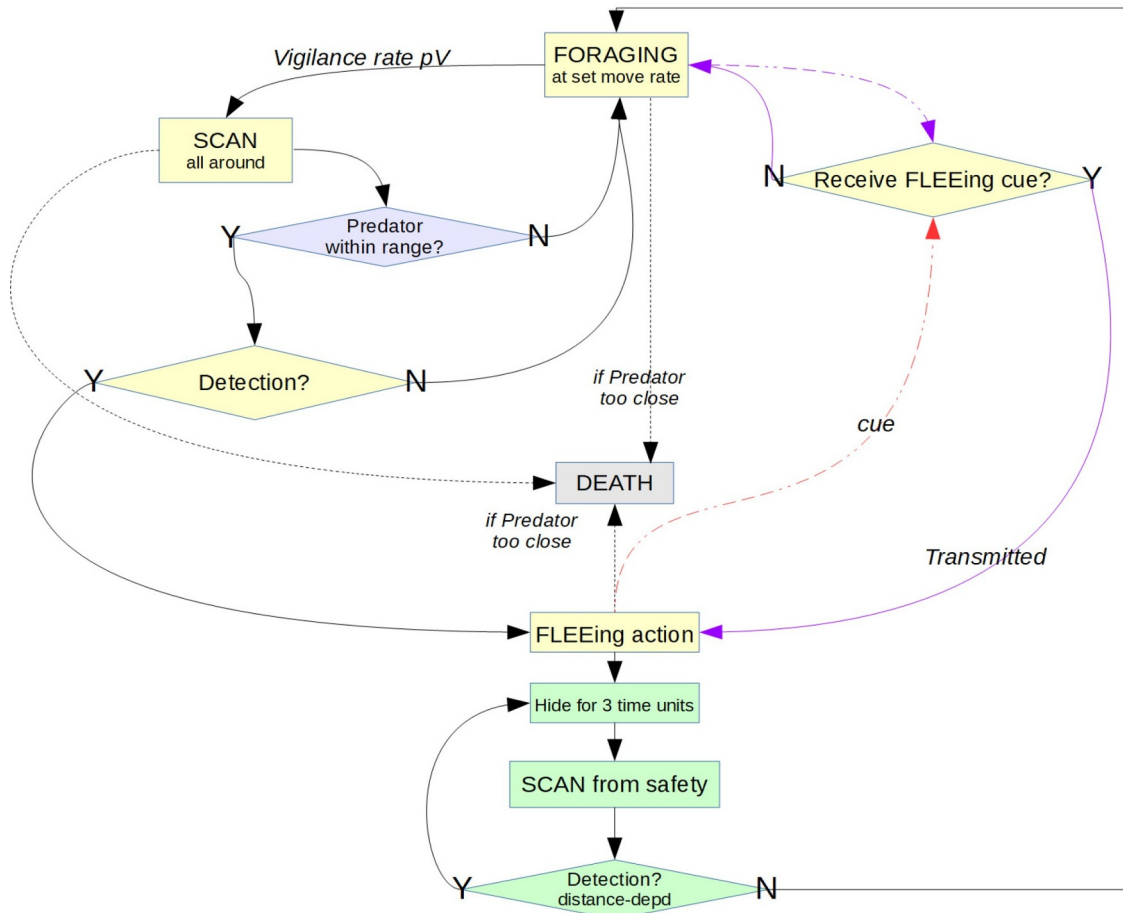
Fig. 3. Behavioural flow chart for individuals in a group. Rectangular boxes: activities or states; diamonds: true/false options. The "FLEEing action" is the moment the cue exists; below Flee: hide in safety, no generation of cues. Solid lines: regular transitions; dotted lines leading to death: the predator came too close. Dot-dashed lines: visual information transmission, an individual notices a fleeing action of another individual. If noticed: copy the flight

Forager movement. All forager movement styles use a random wiggle angle of maximally 10° each way at every move action. During 1 time step the forager forages (or scans) and moves according to movement probability (or it flees). Within one time unit an individual has time to both move and eat, or perform a 360° scan. The individuals stay within distance *r* from the centre; at the border they turn to stay within the area. All movement styles use a random wiggle angle of maximally 10° each way at every move.

○ Regular movement is straight on through the group area; if individuals pass the border they turn and set heading towards a randomly chosen spot within the area and move ahead again. Rate of movement is low (random rate of 0.1) or high (movement at every time-step)

○ Start-stop movement: an individual stays in place for x-1 time units and then moves forward x units of distance in 1 time unit, resulting in a net movement speed of 1. For each individual, x is a random integer between 0 and 4. This means that overshooting the border can occur, since during the forward movement of x units no checking is done.

Predator movement. The predator starts in a corner, targets the nearest forager and moves directly towards it, without wiggle. If an other becomes nearest it switches targets. If the predator gets within 4 units of distance of a forager that is not in safety, it attacks and always kills.

2.3. Simulation Experiments

To investigate the information transmitted at each time-step, simulation experiments were done with the following factors:

- The combination of eye placement and vision-influencing foraging, defining the shape of the field of view (FoV): frontal and lateral, as shown in Fig. 2.
- Size of the field of view (FoV) when not actively scanning for the predator: FoVs of 0° (no reaction to others, so no transmission of the flight cue), 60°-300° (limited transmission) and 360° (perfect transmission). 360° is included to determine maximum reception.
- Group size: 2 up to 20 individuals.
- Movement styles of the patch-bound residential groups staying within a boundary: 1) regular movement at a constant speed and a low rate of 0.1; 2) regular movement at a high probability; and 3) start-stop movement with a high probability.

For this investigation, other factors have been kept equal for all settings of the properties under investigation, such as vigilance rate and distance-dependent detection probability (Fig. 1B), using the equation of Van der Post et al. (2013). Density is set to a constant number of individuals per area, by adapting the radius of the group area to the group size, such that a patch with 20 individuals has a radius of 10 units. The non-attentional viewing range of individuals is such that all individuals of a group remain in range. The attentional vigilance behaviour consists of scanning 360° for a predator, at a set frequency and with distance-dependence over a larger viewing range, represented by a

Table 1
Initialization parameters

Input parameter	Netlogo name	Value range	Definition
Arena		101*101	Distance units (with a distance unit in the order of meters)
Repeats of simulated attacks	repetitions	10 repeats of runs of 1000 attacks	One run collects the summation of results over 1000 attacks
Group size	nr_foragers	2,3,4,5,7,10,15,20 (supplement: 50,75,100,200)	Number of individual foragers
Grouping distance (radius)	grouping_distance, r	10 units of distance	Basis for calculation of density-corrected radius: radius for G = 20
Residential group area radius	denscorr_group	ranges from 3.16 (G = 2), 10 (G = 20), to 31.62 (G = 200)	Radius of the group area, adapted to group size such that area per individual is constant at 15.71 units^2, compensating for density changes
Vigilance rate pV	pV	0.1	probability of performing a vigilance scan
FoV_scan	FoV_scan	360°	FoV of scan for predator (*in supplement appendix E limitations are tested*)
Forager: max. distance for detecting predator	maxdetectdist	50 units of distance	Max. distance for detecting disturbance, with distance-dependent detection probability
Forager: max. reception distance of cues of others	maxview	25 units of distance	Max. reception distance of cues of others, no distance-dependent decay.
Field of View shape	single_field	Yes: Frontal, No: Lateral	Frontal or Lateral (both with a blind angle in the back, and for a split lateral view also an obstructed (to cues coming form other individuals) angle in front
Field of View size	FoV	0°, 60°, 120°, 180°, 240°, 300°, 360°	0° means no reaction to others at all; 360°: perfect transmission, which would represent a fleeing action giving cues by sound or smell
Maximum attack duration	maxdur	300 (+ initial 50)	Maximum attack duration, with a time unit in the order of seconds to minutes, (plus the time before the predator appears)
Movement probability	move_rate	probability of 0.1 or 1	0.1 for residential individuals with a low probability of movement, 1 for all other movement styles, all with 10° random angle
Movement speed	SpeedFs	1 distance unit per time unit	When moving: speed of movement for foragers
Movement angle	move_angle	maximum 10° (only foragers)	each step with an added random wiggle error (only foragers)
Start-stop movement	start-stop	Yes or No	stay in place for x-1 time units, then move forward x units distance in 1 time unit, giving a net speed of 1
Random pause duration	pause_dur	random int., 0 to max. 4	Value of x in start-stop movement style
Hiding time	fleeing-time	3 time units + 1 scanning	Number of time units where a hiding forager stays passive and safe, the 4th tick a scan will be performed
Predators	predator	1 (per attack)	Number of predators (per attack); generated outside visual range of foragers
Speed of predator	SpeedPr	1	1 distance unit per time unit.
Capture distance or kill zone	kill_distance	4 units of distance	Kill is made if predator approaches to within the kill zone of an individual not in safety

sigmoid with increasing probability of detection when a predator is closer.

Visualisation of attacks on groups with different visual fields and move styles and rates are included in the Supplementary Appendix B (Video annotation) and S1-S4 videos. For all videos the same colour indications are used, mapping the states or actions represented in the behavioural schema (Fig. 3).

2.4. Main response variables

The responses of interest in the simulations (Table 2), accumulated over 1000 runs, were: 1) whether successful transmission to the whole group occurred, and 2) whether the predator succeeded in capturing one individual. The two responses are complementary, except for the simulations that ran to the time limit. Therefore, the endpoints for the

simulation runs are either: *capture* of the first individual by the predator; *all-fled,* transmission of a flight cue reaches all individuals of the group. The *all-fled* endpoints show how effective transmission was, and the *capture* endpoints show the group vulnerability and failure of transmission. We look at the risk to the group (number of *captures*), because that shows ineffective transmission in the group. Individual risk (group risk divided by the number of individuals in the group) is less informative because risk per attack to an individual in a group of 20 would only vary between 0 and 0.05.

2.5. Quantifying the visual cue transmission

The main focus of this research is intra-group transmission: either an individual sees the predator directly, or it receives information through flight cues in a chain reaction. Pays et al. (2013, Fig. 1) show a

Table 2
Output and calculated variables

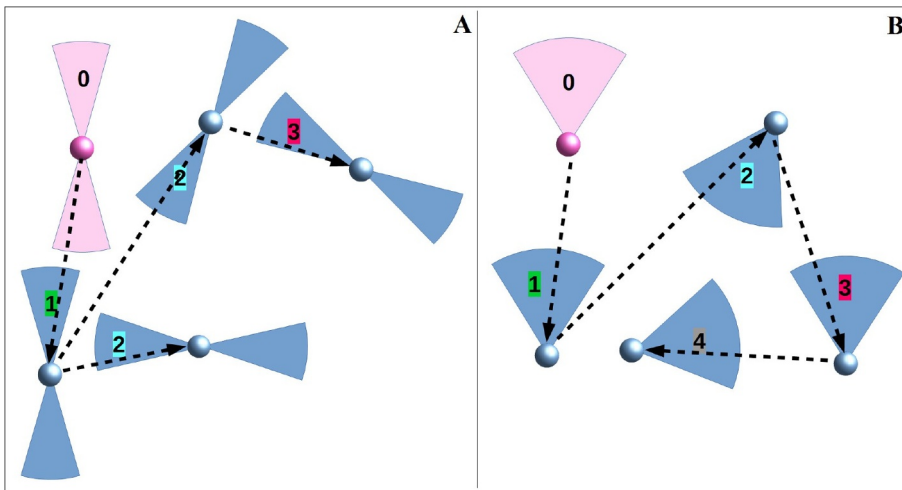| Output variable	Netlogo name	Description
Captures	capture	% of simulations ending in a kill: failure of effective transmission
All-fled	allfled	% of simulations ending in complete transmission, all individuals having fled
None in view	noneinVision	% of time not a single other individual is in view
Detections	spotflee	% of detections followed by a flee and flight cue generation per individual
Successful reception, contagious flight	scareflee	% of flight cues received per detection (of n-1), resulting in contagion of flight
Potentially in view	someinvision	% of other individuals that could have been in view, independent of their behaviour at that moment; measure for the potential maximum information
Average length of the transmission chain	max(SeqL)	average over the group at the end of one simulated attack. If transmission is perfect, length is (n-1)/n, if it is longer then foragers get the cue anew after re-emerging from safety.
Absolute maximum transmission chain length	max(max(SeqL))	Maximum reached over 10 replicates of 1000 runs
Transmission ratio		effectiveness: calculated as the ratio of Successful flight cue reception to what was Potentially in view

Fig. 4. Transmission chains for individuals with lateral (A) or frontal (B) visual fields, with total FoV of 60° in both cases. The lighter individual (number 0) detects the predator, and then others receive the flight cue from the previous one in order of numbering. The transmission chain is indicated by the arrows. All individuals are close enough to each other to be within visual range; the angles impose limits to reception.

very nice chain of transmission, a domino-like effect, in their observations of a group of eastern grey kangaroos after detection of a presented predation threat. Retransmission in our model is illustrated in Fig. 4 for individuals with a lateral (A) or frontal (B) visual field with a total field of view of 60°. Individuals are numbered in the order in which they receive the flight cue, resulting for the depicted situation in a maximum chain length of 3 or 4, respectively.

To quantify this intra-group transmission, we need to know i) the total number of individuals present in the visual field, and ii) how many individuals actually notice and react to a flight cue. For i), the individuals in view are counted at every time-step, independent of their action at that moment. This number is used to calculate the maximum percentage of individuals in view, independent of their behaviour (*Potentially in view*), that is, including the ones that were in that location just before or after fleeing, but now are not in a position to generate cues. For ii) we counted predator detections and how often a fleeing action was copied by the potential reactors (n−1). Number of copies divided by number of detections gives the reactions to each detection (*Successful reception*).

Transmission is quantified as the ratio of information present to the maximum information: that is, the number of times a flight cue was successfully received (*Actual reaction*) to the number of individuals that were in the visual field independent of their behaviour, including the ones that were sheltering (*Potentially in view*). If this transmission ratio is lower than 1, there is under-reaction when some others did not generate warning cues, even though they were (just before or after) in a location in view. This situation occurs when an individual was captured, or when an individual had fled and stayed quiet or hidden for a time; during this time no cues are generated; cue generation happens only at the time of flight itself (Fig. 3). In that situation transmission only reaches a part of the group; a side effect is, that on average the simulation takes longer to stop, after a higher number of detections. If the total number of individuals in view is smaller than the total number of reactions to a detection, resulting in a transmission ratio above 1, then there is retransmission. This occurs when individuals come out of safety, after checking whether a predator was in sight and (erroneously) not spotting one, and then again receive a flight cue.

To check whether retransmission occurs, and to describe the transmission chains, two measurements were added: the average length of the chains, and the maximum length of transmission chains that was reached in the 1000 runs. For the length of the transmission chains the number of links is counted: the detector, any individual that detected a predator during its vigilance scan, is number 0, the ones that directly react to the flee by the detector are 1 link away, and the ones reacting to those ones are 2 links away. In Fig. 4, the average chain length is 1.6 (A: $(0+1+2+2+3)/5$) and 2 (B: $(0+1+2+3+4)/5$). The expected

average length (per individual) if transmission is perfect is (n-1)/n. A length below 1 does not necessarily mean that there is no retransmission at all, but a length above 1 is only achievable with retransmission.

3. Results

3.1. Patch-bound residential groups

The frequency of the simulated attacks ending with ***All-fled***, all individuals fleeing from the predator, is shown in Fig. 5 (with numerical representation in Table 3-I). For patch-bound residential groups, percentage of ***captures*** give the inverse pattern, since no stops by time-out occur.

Figure 5 makes clear that, for a residential group moving around in a patch, a lateral visual field is more effective in noticing a flight cue than a frontal continuous field of the same size, and that the largest difference is at a FoV of 120°. Figure 5 also shows that in very small groups the probability of being killed depends less on transmission than in larger groups. It must be noted that **individual risk** is highest in the smallest group. See for the graph for the individual predation risk Appendix C, Fig. C.1B.

We expected that the results would be affected by different movement probabilities and patterns of repositioning relative to other individuals. A high movement probability of 1 was tested, as well as a start-stop movement style. The advantage of a lateral field shape over a frontal one is also present for the movement probability of 1 (Fig. 6A): the lateral shape is associated with higher frequencies of all individuals fleeing than the frontal shape, thereby reducing captures. With the start-stop movement style (Fig. 6B), the differences between frontal and lateral fields in number of ***All-fled*** decreases, and in small groups a frontal field actually provides better transmission for narrower FoVs, including 180°. When movement probability is high, compared to the low probability of 0.1, the disadvantage of a frontal visual field decreases.

In summary, our simulations show that in residential groups with different movement styles, a lateral field of view is better in the tested cases, except in small groups with a start-stop movement style.

3.2. Fields of view with similar transmission in residential groups

A residential group (Fig. 7, A) with either a frontal visual field of 300° or a lateral field of 240° shows virtually the same intra-group transmission. The difference between these two situations is a blind gap of 60° in front, leaving equal angles for perceiving cues with the remaining visual field. Even when the blind angles are all 90° (Fig. 7, B), only in small groups there is a disadvantage for the individuals with a
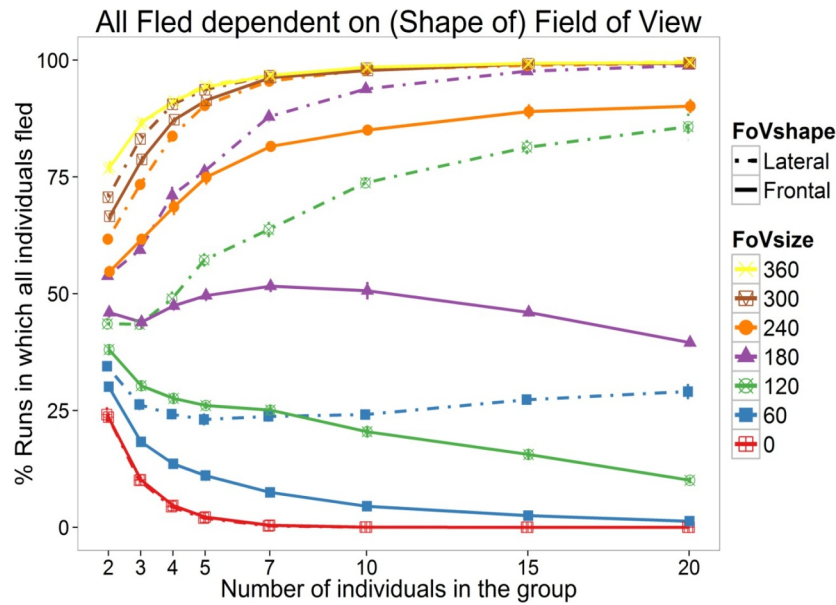
Fig. 5. Number of runs out of 1000 in which All-fled, individuals have movement rate 0.1 and move angle 10°. Frontal and lateral fields of view (FoVs) with varied total visual angles. Dashed lines (lateral) are always above full lines (frontal) for the same FoV-size. 10 repeats; bars are confidence intervals.

smaller total field, that is, the lateral visual field. The cue reception lost in the frontal "blind" angle apparently hardly influences transmission if the visual field is wide enough.

3.3. Quantification of visual cue transmission

Table 3 shows the relation between ***All-fled***, the result of transmission reaching all members of a group (Table 3-I), and seven other transmission-related variables for the patch-bound residential group with movement probability 0.1 and move angle 10°. ***None in View*** (Table 3-II) gives the time where individuals have no other individual in their visual field; this number is lower for a lateral view. In this patch-bound setting an explanation for the advantage of the area being lateral to oneself is in the uncoordinated movement in the patch; when your view is only frontal, at the border you look out and do not see others; with a lateral view you could see at least others next to you near that border.

The number of ***Detections*** (Table 3-III) per individual is also indicative of the quality of transmission: a higher number means that the predator did not quickly kill, and also that not all individuals fled after a detection.

The percentage of ***Successful cue reception*** (Table 3-IV) is at maximum 100%, with perfect transmission, but in actuality 100% is not reached. This has two reasons: captures still occur, and more than one individual can spot the predator independently at the same moment.

The percentage of individuals in view independent of their behaviour (***Potentially in view)*** (Table 3-V) indicates how many individuals could generate information. This percentage depends on the size and shape of the Field of View, but is nearly independent of the number of individuals present in a group. With a random placement of individuals one would expect 50% for a FoV of 180°, but this neglects the effects of movement on spatial distribution of animals. It shows that with this movement pattern a lateral field contains more other individuals than a frontal field.

Transmission Ratio (Table 3-VI) is the ratio of information received to the information maximally generated within the visual fields: in small groups there is no strong effect of shape of the field of view, but for larger groups clearly a lateral field is more effective. Strong differences in Transmission Ratios between lateral and frontal fields exist at a FoV of 120° or 180°; the larger the group is, the stronger the advantage for a lateral field. The variables influencing this ratio are several: the

number of initial detections, the number in view, the number that already fled contagiously just before. If transmission reaches only part of the group, the probability that new information is generated goes down. This also means that the simulated attack lasts longer: If not all foragers are warned after one detection, in the next time step the amount of information is also diminished, but this decrease can be partly relieved with some time delay, if retransmission occurs.

When transmission is perfect in a group of 10, the ***Average chain length*** is 9/10 (Table 3-VII); if the average is lower than $((n-1)/n)$ there could be retransmission, as illustrated in Fig. 4, but a value above $((n-1)/n)$ can only be reached if there is retransmission. Table 3-VII shows that retransmission is more frequent with a lateral visual field (Table 3-VI) than with a frontal one. If there are more flight copies than expected from the number of individuals in view, this indicates that retransmission occurs (***Actual Reaction***, Table 3-IV). With a frontal view the ***Transmission Ratio*** is much lower, mostly below 1, so transmission is less effective, also evident in the increased number of ***Detections*** needed to reach an endpoint of a simulation (Table 3-IV): chains peter out too early. The highest average lengths are for groups of 20, with lateral field of 120° or a frontal field of 240°.

The ***Maximum length*** (Table 3-VII):of a transmission chain is measured as the longest chain of cue transmission occurring in the 1000 attacks. The maximum length can be longer than the number of individuals, caused by the limited duration of a flee (see Fig. 3); the individual returns from fleeing when it does not re-detect the predator, and then may notice a cue that is still being transmitted, so information can be picked up at more points in time. The ***maximum length*** exceeds the number of individuals at smaller FoVs for lateral compared to frontal fields, starting from (7-)10 individuals. For a lateral field the chains are longest, nearly 30 links at group size 20 and FoV of 60°, for frontal fields nearly 21 links for groups of 20 with a frontal field of 180°.

The ***Absolute maximum length*** of the transmission chain (Table 3-VIII): the maximum length for a lateral view is at a smaller visual angle than the maximum length for a frontal view. Both are in the largest group of 20, since there the chances are lowest that all detect the threat simultaneously

Table 4 shows the ***Average chain lengths*** for the start-stop movement style, to compare to ***Average chain lengths*** for the regular style with movement probability 0.1 (Table 3-VII). The *chain lengths* for lateral and frontal fields are more similar for the start-stop movement style than for the regular movement style; the total length of chain for

Table 3

The output variables of the model describing effectiveness of transmission in a residential group with constant movement probability 0.1 and move angle 10°. The settings where retransmission occurs (VI), or in which the average length exceeds the average for perfect transmission (VII), have been framed in black. Shading code: from dark to light: a gradient towards positive outcome for the individuals or group. The third column gives the differences (values for lateral - values for frontal shape); positive: blue bars, negative: red bars.

NrIndiv	Lateral							Frontal							Lateral-Frontal						
	0°	60°	120°	180°	240°	300°	360°	0°	60°	120°	180°	240°	300°	360°	0°	60°	120°	180°	240°	300°	360°
I	**% Simulations that ended with all individuals having fled (All Fled)**																				
2	24.1	34.5	43.6	53.8	61.7	70.6	76.6	23.6	30.1	38.0	46.0	54.7	66.6	77.1	0.6	4.4	5.5	7.8	7.0	4.1	-0.5
3	10.1	26.3	43.5	59.4	73.4	83.1	86.1	10.2	18.3	30.3	43.9	61.7	78.7	86.7	-0.1	8.0	13.2	15.5	11.7	4.4	-0.6
4	4.4	24.2	48.9	71.1	83.7	90.5	91.0	4.7	13.6	27.6	47.4	68.6	87.2	91.3	-0.3	10.6	21.3	23.6	15.1	3.3	-0.3
5	2.0	23.1	57.2	76.2	90.3	93.7	94.6	2.2	11.1	26.1	49.6	74.9	91.4	94.3	-0.2	12.0	31.1	26.6	15.4	2.3	0.3
7	0.3	23.7	63.7	87.9	95.5	96.7	96.7	0.4	7.5	25.1	51.6	81.5	96.3	96.8	-0.1	16.3	38.6	36.3	14.0	0.4	0.0
10	0.0	24.1	73.7	93.8	97.9	98.3	98.5	0.0	4.5	20.5	50.6	85.0	97.8	98.5	0.0	19.6	53.3	43.2	12.9	0.5	0.0
15	0.0	27.3	81.4	97.6	98.9	99.2	99.2	0.0	2.5	15.6	46.0	89.0	99.2	99.3	0.0	24.8	65.8	51.6	9.9	0.0	-0.1
20	0.0	29.1	85.7	98.8	99.3	99.4	99.6	0.0	1.3	10.1	39.5	90.1	99.3	99.5	0.0	27.8	75.7	59.3	9.2	0.1	0.2
II	**% Time no others are in view (None in view)**																				
2	100	84.4	68.7	52.4	35.6	17.9	0	100	89.0	77.3	62.4	45.2	24.7	0	0	-4.6	-8.6	-10.0	-9.6	-6.8	0
3	100	71.1	48.3	29.9	14.2	3.8	0	100	80.2	63.5	46.0	27.4	9.0	0	0	-9.1	-15.2	-16.1	-13.2	-5.2	0
4	100	60.2	34.9	17.4	6.2	0.9	0	100	72.2	52.7	35.3	18.4	3.8	0	0	-12.1	-17.9	-17.8	-12.2	-2.9	0
5	100	52.2	25.5	12.1	3.3	0.3	0	100	66.2	47.0	29.4	14.4	2.2	0	0	-14.1	-21.5	-17.3	-11.1	-1.9	0
7	100	39.8	16.3	5.6	1.0	0.0	0	100	57.8	38.6	23.1	9.5	0.8	0	0	-17.9	-22.4	-17.5	-8.5	-0.8	0
10	100	27.4	9.1	2.4	0.3	0.0	0	100	47.4	29.4	16.6	5.6	0.2	0	0	-20.0	-20.3	-14.2	-5.4	-0.2	0
15	100	16.9	4.7	0.9	0.1	0.0	0	100	40.6	23.9	12.7	3.3	0.0	0	0	-23.6	-19.2	-11.8	-3.3	0.0	0
20	100	11.5	2.9	0.4	0.0	0.0	0	100	36.6	20.6	10.3	2.2	0.0	0	0	-25.1	-17.7	-9.9	-2.2	0.0	0
III	**% Detections and flight cue generation per individual**																				
2	79.7	71.8	65.4	58.7	51.6	45.8	39.0	78.1	74.2	69.8	64.1	57.6	48.7	39.2	1.6	-2.4	-4.4	-5.4	-6.0	-3.0	-0.2
3	81.6	75.3	65.4	54.2	42.3	33.4	29.6	81.9	78.4	73.6	65.6	54.5	38.4	29.7	-0.4	-3.1	-8.1	-11.4	-12.2	-5.0	-0.1
4	77.2	74.8	60.6	45.2	31.6	25.0	23.5	78.0	79.0	76.3	64.3	47.9	28.2	23.6	-0.8	-4.2	-15.7	-19.1	-16.3	-3.2	-0.1
5	73.1	74.5	55.4	40.7	24.8	20.2	19.7	73.8	77.2	77.4	64.7	42.6	22.6	19.6	-0.8	-2.8	-22.0	-24.0	-17.8	-2.4	0.1
7	64.8	73.5	52.4	26.9	16.8	14.8	14.5	64.7	75.1	81.2	65.6	37.6	15.7	14.5	0.1	-1.6	-28.8	-38.7	-20.8	-1.0	0.0
10	54.6	74.2	46.5	19.8	11.2	10.6	10.3	54.5	72.0	81.8	70.9	32.6	11.1	10.4	0.1	2.2	-35.3	-51.1	-21.4	-0.5	0.0
15	43.7	79.2	37.0	10.7	7.3	7.1	7.0	43.4	69.6	85.8	76.7	27.2	7.2	7.0	0.3	9.7	-48.8	-66.0	-19.9	-0.1	0.0
20	36.7	82.4	29.3	7.1	5.4	5.4	5.3	36.8	65.4	83.3	84.3	22.6	5.4	5.3	0.0	17.1	-54.0	-77.2	-17.2	0.0	0.0
IV	**% Successful flight cue reception per Detection (Actual reaction)**																				
2	0	10.8	21.6	35.8	52.0	72.2	96.5	0	6.2	14.1	24.2	38.1	61.6	96.7	0	4.6	7.4	11.6	13.8	10.6	-0.3
3	0	11.5	24.0	39.0	59.6	83.0	95.6	0	6.7	14.9	25.4	41.2	70.2	96.1	0	4.9	9.1	13.7	18.4	12.7	-0.5
4	0	12.9	27.6	46.5	69.9	90.1	95.7	0	7.3	15.8	27.8	45.0	79.3	95.6	0	5.6	11.8	18.7	24.9	10.8	0.0
5	0	13.7	31.0	46.5	76.1	92.2	95.0	0	8.5	16.4	28.1	46.8	83.2	95.1	0	5.2	14.5	18.4	29.3	9.0	0.0
7	0	14.3	30.1	56.1	83.3	92.6	94.5	0	9.1	16.6	26.1	44.7	88.6	94.4	0	5.2	13.5	30.0	38.6	4.0	0.1
10	0	14.6	29.3	56.7	87.7	92.3	94.8	0	9.8	15.8	22.5	40.9	88.8	94.3	0	4.8	13.6	34.2	46.8	3.5	0.4
15	0	14.0	28.4	67.7	90.4	93.0	94.3	0	10.3	14.0	18.5	36.7	91.9	94.1	0	3.7	14.4	49.2	53.7	1.2	0.2
20	0	13.1	28.1	74.1	91.1	92.6	94.5	0	10.5	12.8	15.5	34.6	92.4	94.2	0	2.6	15.3	58.5	56.5	0.2	0.3
V	**% Other Individuals that could have been in view (Potentially in view)**																				
2	0	15.7	31.4	47.7	64.6	82.2	100	0	11.0	22.7	37.6	54.8	75.3	100	0	4.7	8.7	10.2	9.7	6.9	0
3	0	16.2	31.9	47.8	65.3	82.5	100	0	11.3	23.4	37.8	55.3	76.4	100	0	4.9	8.5	10.0	10.0	6.1	0
4	0	16.4	32.4	48.8	66.0	82.8	100	0	12.0	25.0	39.7	56.8	78.1	100	0	4.4	7.4	9.1	9.2	4.7	0
5	0	16.1	32.9	47.4	65.2	82.6	100	0	12.3	24.9	39.9	56.5	77.5	100	0	3.8	8.0	7.5	8.7	5.1	0
7	0	15.9	31.8	48.3	65.1	82.6	100	0	12.5	25.6	40.2	56.8	77.6	100	0	3.4	6.1	8.1	8.3	5.0	0
10	0	15.9	31.6	47.8	65.2	82.3	100	0	13.5	27.4	42.1	58.5	78.4	100	0	2.4	4.1	5.8	6.7	3.9	0
15	0	15.5	31.0	47.5	64.7	81.9	100	0	13.3	27.1	41.4	57.7	77.3	100	0	2.2	3.9	6.1	7.0	4.6	0
20	0	15.2	31.0	47.0	64.0	81.9	100	0	13.0	26.8	40.8	57.4	77.1	100	0	2.2	4.2	6.2	6.7	4.8	0.00
VI	**Transmission Ratio: Actual reaction / Potentially in view**																				
2	-	0.69	0.69	0.75	0.80	0.88	0.96	-	0.57	0.63	0.64	0.70	0.82	0.97	-	0.12	0.06	0.11	0.11	0.06	0.0
3	-	0.71	0.75	0.82	0.91	1.01	0.96	-	0.59	0.64	0.67	0.75	0.92	0.96	-	0.12	0.11	0.15	0.17	0.09	0.0
4	-	0.79	0.85	0.95	1.06	1.09	0.96	-	0.61	0.63	0.70	0.79	1.02	0.96	-	0.18	0.22	0.25	0.27	0.07	0.0
5	-	0.85	0.94	0.98	1.17	1.12	0.95	-	0.69	0.66	0.70	0.83	1.07	0.95	-	0.16	0.28	0.28	0.34	0.04	0.0
7	-	0.90	0.95	1.16	1.28	1.12	0.95	-	0.73	0.65	0.65	0.79	1.14	0.94	-	0.17	0.30	0.51	0.49	-0.02	0.0
10	-	0.91	0.93	1.18	1.34	1.12	0.95	-	0.73	0.57	0.53	0.70	1.13	0.94	-	0.19	0.35	0.65	0.65	-0.01	0.0
15	-	0.90	0.92	1.43	1.40	1.14	0.94	-	0.78	0.52	0.45	0.64	1.19	0.94	-	0.13	0.40	0.98	0.76	-0.05	0.0
20	-	0.86	0.91	1.58	1.42	1.13	0.94	-	0.80	0.48	0.38	0.60	1.20	0.94	-	0.06	0.43	1.20	0.82	-0.07	0.0
VII	**Average Length of Transmission Chain**																				
2	0	0.08	0.14	0.21	0.27	0.33	0.38	0	0.05	0.10	0.15	0.22	0.30	0.38	0	0.03	0.04	0.06	0.05	0.03	0.0
3	0	0.12	0.27	0.42	0.54	0.60	0.57	0	0.06	0.15	0.27	0.42	0.57	0.57	0	0.06	0.12	0.15	0.12	0.04	0.0
4	0	0.18	0.44	0.66	0.77	0.77	0.67	0	0.08	0.21	0.40	0.60	0.75	0.68	0	0.11	0.23	0.27	0.18	0.02	0.0
5	0	0.24	0.63	0.83	0.92	0.85	0.75	0	0.11	0.26	0.50	0.74	0.85	0.75	0	0.13	0.37	0.33	0.17	0.01	0.0
7	0	0.37	0.87	1.09	1.07	0.94	0.82	0	0.16	0.36	0.62	0.91	0.96	0.82	0	0.22	0.51	0.47	0.15	-0.02	0.0
10	0	0.55	1.14	1.28	1.16	1.02	0.88	0	0.24	0.45	0.73	1.05	1.04	0.88	0	0.31	0.69	0.55	0.11	-0.02	0.0
15	0	0.83	1.42	1.41	1.22	1.08	0.92	0	0.41	0.59	0.84	1.21	1.10	0.92	0	0.42	0.83	0.56	0.02	-0.03	0.0
20	0	1.08	1.57	1.45	1.27	1.10	0.94	0	0.57	0.70	0.94	1.29	1.13	0.94	0	0.51	0.86	0.51	-0.02	-0.03	0.0
VIII	**Absolute Maximum Length of Transmission Chain**																				
2	0	1.0	1.0	1.0	1.0	1.0	1	0	1.0	1.0	1.0	1.0	1.0	1	0	0	0	0	0	0	0
3	0	2.0	2.0	2.0	2.0	2.0	1	0	2.0	2.0	2.0	2.0	2.0	1	0	0	0	0	0	0	0
4	0	3.0	3.0	3.0	3.0	3.0	1	0	3.0	3.0	3.0	3.0	3.0	1	0	0	0	0	0	0	0
5	0	3.9	4.0	4.0	3.9	3.4	1	0	3.6	3.8	4.0	4.0	3.9	1	0	0.3	0.2	0	-0.1	-0.5	0
7	0	5.5	5.0	5.3	4.8	2.9	1	0	4.1	4.8	4.9	5.6	3.9	1	0	1.4	0.2	0.4	-0.8	-1	0
10	0	9.7	13.5	9.9	4.3	2.4	1	0	5.1	6.4	11.7	9.6	4.0	1	0	4.6	7.1	-1.8	-5.3	-1.6	0
15	0	23.7	22.5	7.4	3.4	2.0	1	0	9.0	13.1	14.2	16.3	3.1	1	0	14.7	9.4	-6.8	-12.9	-1.1	0
20	0	27.4	23.0	8.7	3.0	2.0	1	0	15.0	17.9	22.9	14.4	3.1	1	0	12.4	5.1	-14.2	-11.4	-1.1	0

all lateral fields hardly changes, but for frontal fields the increase in length was over 35%. This difference was also seen in the **captures** (Fig. 5) for regular low movement probability, where also lateral and frontal fields differed more than in the start-stop movement style (Fig. 6).

Supplementary Appendix D gives the tables for residential groups with different movement styles, to compare to Table 3.

3.4. Results on additional simulation experiments

We checked what happens when the attentional detection scan for the predator is also limited to the same visual field limitations as used for non-attentional reception instead of the standard 360° scan. A limited scan led to more captures than a 360° scan if the non-attentional reception was also limited, but perfect transmission was apparently more important than a 360° vigilance scan, except in the smallest
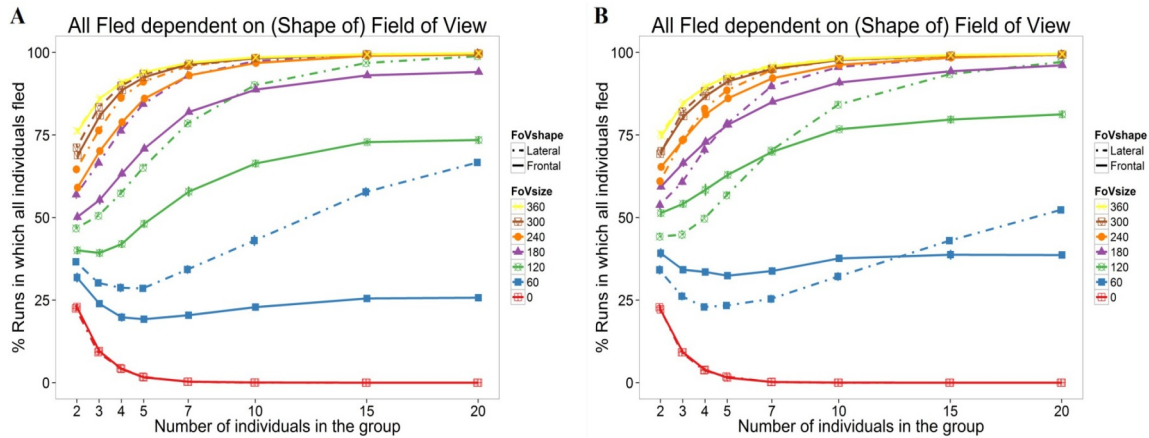
Fig. 6. Percentage of All-fled over 1000 runs A: with high movement probability 1.0. B: individuals move in start-stop style.

groups. Supplementary Appendix E: graphs of the effects of the standard 360° scan (Fig. E.1A and 2A) are compared to limitation of both scan and transmission (Fig. E.1B), and compared to a vigilance scan limited by the visual field but with perfect transmission (Fig. E.2B).

When the model was run with larger groups (50-200), we did not change the density or the maximum reception range of individuals. In consequence, when the group size is larger than 20, some individuals can be out of viewing range. See Supplementary Appendix F for the resulting figures and table, and Appendix B (the video read-me) and videos S5-S6 for a visualization of attacks on residential groups of 100 individuals with a frontal or lateral visual field. With these settings, for residential groups the transition from insufficient transmission to complete transmission became much more sharply defined at around 60° for a lateral visual field but around 180° for a frontal field.

3.5. Sensitivity analysis results

The effect of different settings for initial parameters: see Table G.1 of Appendix G of the Supplementary Material, with averages of the results for the 56 settings (8 group sizes x 7 visual field sizes), and Table G.2 for the percentage of All-fled and average transmission chain length per visual field shape for groups of seven individuals. The pattern for the groups of seven is very similar to that for the overall averages.

Increasing the parameter setting for vigilance probability pV, total detection probabilities or a smaller kill zone leads to a higher percentage of All-fled. Increased detection sometimes goes with unchanged transmission (pV), but at other settings transmission is worse (higher total detection probability). The difference between a linear and an S-

curve both with 0.5 total detection probability is most noticeable in the smaller visual fields. Some other parameter changes decrease information transmission (see Table G.1 and G.2), such as a faster predator (speedpr 2), being too close together making it easy for the predator to switch to another prey (radius of group area 3 with a small visual field), being too far apart to see enough others (radius of group area 35), or not seeing enough others (maxview 5). The results remain qualitatively the same for all parameter variations. The shape of the visual field becomes less important with better individual detection of the predator. When individuals moved aligned in wide groups, lateral vision kept more others in view; the only exception was when individuals moved in narrow groups, then frontal vision had more individuals within the visual field (Supplementary Appendix H).

4. Discussion

We tested the effects of shapes and sizes of fields of view (FoV) on information received by individuals, thereby influencing survival. The information was transmitted by visual cues generated by other individuals fleeing after attentional detection of a predator, at times when the recipients were foraging and not actively scanning for predators. We tested these effects in a spatial model that simulates vigilant individuals living under predation.

4.1. Effect of visual field shape

As argued in the introduction, differences in shape and size of the field of view are due to a combination of visual morphology and
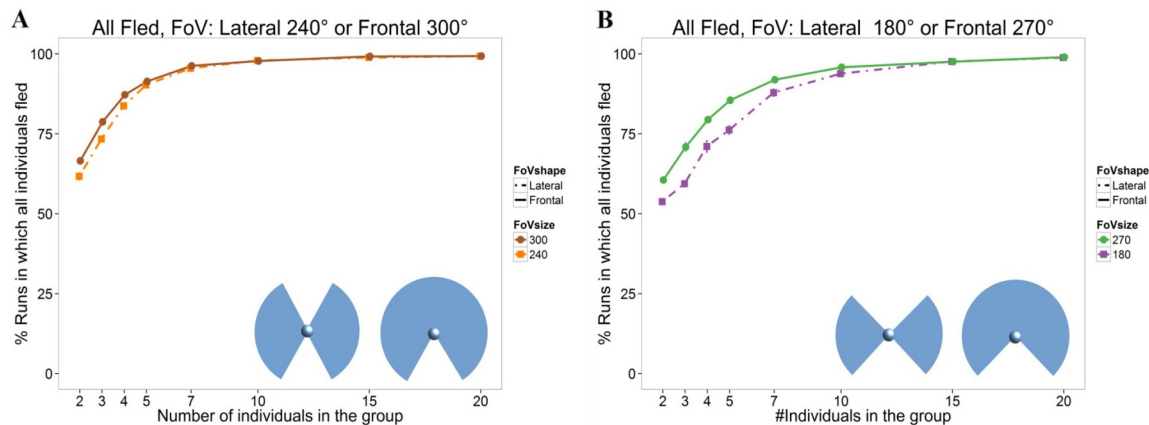

Fig. 7. Percentage of All-fled in residential groups that move regularly at low movement probability 0.1. In both situations the lateral fields has an extra front obstructed angle of the size of the back blind angle of the frontal fields.

Table 4
Average length of transmission chain (start-stop movement style). The settings in which the average length exceeds the average for perfect transmission have been framed.

Nr.Indiv	Lateral							Frontal						
	0°	60°	120°	180°	240°	300°	360°	0°	60°	120°	180°	240°	300°	360°
Start-stop: Average Length of Transmission Chain														
2	0	0.1	0.2	0.2	0.3	0.3	0.4	0	0.1	0.2	0.3	0.3	0.3	0.4
3	0	0.1	0.3	0.4	0.5	0.6	0.6	0	0.2	0.3	0.5	0.5	0.6	0.6
4	0	0.2	0.4	0.7	0.8	0.8	0.7	0	0.3	0.5	0.6	0.7	0.7	0.7
5	0	0.2	0.6	0.9	0.9	0.9	0.7	0	0.3	0.6	0.8	0.9	0.9	0.7
7	0	0.4	1.0	1.2	1.1	1.0	0.8	0	0.5	0.9	1.1	1.1	1.0	0.8
10	0	0.6	1.3	1.4	1.2	1.0	0.9	0	0.7	1.1	1.3	1.2	1.0	0.9
15	0	1.0	1.6	1.4	1.2	1.1	0.9	0	0.9	1.4	1.4	1.3	1.1	0.9
20	0	1.2	1.7	1.5	1.3	1.1	0.9	0	1.1	1.5	1.5	1.3	1.1	0.9

behaviour. Reception of an informative cue depends on the size and shape of the field of view in combination with orientation towards the generator of that cue, so in our simulation experiments we varied group sizes and affected positions and orientations of individuals towards each other through manipulation of movement styles and movement frequencies.

A lateral visual field is shown to be more advantageous than a frontal field for transmitting warning cues in patch-bound residential groups with a movement probability of 0.1, over the whole range of tested limitations of the fields of view (FoV), between 60° and 300° (see Fig. 5 and Table 3), but the larger differences are seen at sizes of the FoV that are below what is found in nature. By this better transmission for lateral visual fields the fleeing behaviour becomes more synchronized, giving the predator less reason to remain because of the loss of targets.

Fig. 7 shows that an individual with a wider visual field, caused by eyes placed laterally, but having a "blind", obstructed, angle in front that precludes reception of more distant cues, can put its nose to its food and still perceive enough cues to reach optimal reception.

In patch-bound residential groups, the advantage of having a lateral FoV is smaller when frequency of movement is higher and the individuals reorient themselves more frequently. Apparently, a higher frequency of position shifts relative to others leads to more occasions for cue reception.

The higher escape rate for individuals with a frontal field when using the start-stop movement (Fig. 6B), rather than regular movement (Fig. 6A), may partly be a side-effect of the movement style: individuals can overshoot the boundary, with the result that on average individuals are further out from the centre than with the regular movement. This means that these individuals with a frontal field have an improved view of the others within the group area at the moment of turning back, and those with a lateral view more often have an empty visual field.

For the smallest groups the shape of the visual field is not important, as long as bouts of vigilance are based on a 360° scan. Their safety depends more on their group not being discovered by the predator at all; in a group of two the probability of both individuals detecting the danger separately is relatively high, as is shown by the probability of **All-fled** when no transmission is present. In larger groups, a slight decrease in vigilance could increase foraging time without leading to a much larger individual risk. Individual risk depends also on the hunting behaviour of the predator: if it kills more than one individual per attack, the risk of course increases.

While a 360° visual field for cue reception of other group members is unrealistic, it nevertheless represents what happens if a flight generates sounds. Sound would work over the same local distances and speed as visual cues. A 360° perceptual field also could represent smell as a warning cue; however, for smell other aspects than speed of the cue could be important: for instance the duration of the cue is more extended, so a cue by smell is more an indication of the presence of danger than an actual detection of danger, as described by Chivers et al. (2014). Signals are defined as being optional, therefore they require more cognition than the cue transmission modelled here.

4.2. Measuring cue reception

The quantification of the cue reception provides an insight into the transmission chains, showing how information spreads through the group. The transmission chain lengths at smaller fields of view are longest for the lateral visual field shape, indicating that here information passes quite effectively at low visual angles. The chain lengths and the transmission ratio show that cues received non-attentionally and passed on could be a mechanism for the advantage of a lateral visual field for groups under predation.

It would be interesting to check the importance of this mechanism for small groups in the field, and see whether the described transmission can be recorded and linked to visual field sizes, foraging, attentional vigilance behaviours, predation pressure and movement patterns. High-speed cameras would be needed because of the expected high speed of the cue transmission; simultaneous sound recording is essential, to be able to distinguish between modes of transmission. In field experiments, sounds and smell interfere with visual information. However, it is possible to perform experiments in the lab, in which a single animal is in a position to detect a threat, whereas others, in the process of foraging, cannot detect this threat, but can instead be warned by visual information transmission.

4.3. Conclusion

In general, having a laterally directed visual field enhances survival in group-living animals under predation. In this study, this benefit can only be attributed to the effectiveness of transmission of visual warning cues within the group, since detection of the predator is removed as a factor by using a 360° vigilance scan for all settings.

The strongest advantage of lateral vision occurs at smaller sizes of the total visual field and in larger groups; individuals in the smallest groups do not get enough cues from their few group mates. Limitation of the visual field existing at moments when animals are not actively scanning around arises from the combination of morphology and behaviour. Losing a part of the visual field for cues from the intermediate distance during foraging still allows sufficient reception of flight cues if the field is large enough, since non-attentional cue reception does not need extreme focusing or binary vision.

However, when it comes to maximising the probability of detecting a predator, the use of the whole visual field, and therefore attention, is necessary, since a predator could come from any direction. The advantage of using the lateral part of the visual field for non-attentional reception of cues about danger is shaped by the fact that the two blind angles of the lateral field are half the size of the blind angle of the frontal field, combined with the fact that more information comes in from the sides than from the front (given incoming information from any direction).

The benefit of non-attentional reception of cues would drive the evolution of the visual field to become ever larger. However, costs of a large visual field through more lateral placement of the eyes are high, in loss of binocular vision used for feeding, moving or detection

(Martin, 2017). These needs for good binocular vision exert a much more immediate selection pressure than the need for cue reception in a group, posing upper limits to expansion of the visual field. This does not prevent the processes described in this paper to exert a strong influence on survival. Our results show that, for groups of individuals that are in visual range of others, the visual field can be size limited and still have optimal reception of cues. The costs of good cue reception itself lie in overreaction: if a detector reacted by fleeing not only to predators but also to harmless disturbances, increasing reception of cues would increase of loss of foraging time without the benefit of increasing survival.

Our tests of the mechanism of "collective detection", as defined by Lima (1995), included that visual cues to the detected presence of danger were received non-attentionally, and reception of these cues often is limited, but excluded individuals attentionally monitoring others. Our results indicate that after a detection of danger and flight cue generation it is uncommon that all other group members receive this cue and flee. These results point to an explanation for the observations described by Lima (1995): one bird detecting danger and fleeing, and only some others reacting. The results also agree with the observations of Butler et al. (2016): starlings significantly oriented their high-acuity vision towards a threat but not towards their conspecifics. Caraco & Bayham (1982) also found that in the observed house sparrows, the sparrows oriented themselves such that they can keep track of the neighbours. By doing so they improve their reception of flight cues. Given a constant vigilance rate, both the amount of information collected and the transmission of this information is improved in larger groups, both directly and indirectly leading to more disturbance and flight from predators.

The point asserted here via this model is that this reception of others' reactions to danger is enough to give an advantage to group living, and that this does not require a completely unobstructed visual field, or active attentional monitoring. This phenomenon of non-attentional cue reception and its benefits (and costs) exists in those species that live in groups and react to visual information.

Favreau et al. (2010) found that social vigilance of female kangaroos, during which they look at other group members, increased and anti-predator vigilance decreased with the size of the group. Favreau and colleagues contrasted costs of social vigilance directed to others in the group with the advantages of the risk dilution and of anti-predator vigilance. We conclude that social vigilance, on top of the non-attentional cue reception, also has a function in anti-predator cue transmission.

When a group is formed under predation (Van der Post, 2008) or under influence of food preferences, group-living is promoted by good intra-group transmission of warning cues, in our case by way of large fields of view, or, if the field of view is smaller, a lateral visual field. This of course only holds for directional visual cues, not for auditory cues or alarm calls.

Therefore, with a frontal eye placement one would expect auditory signals, such as alarm calls, to be more important (evolve sooner) in the larger groups, while small groups would be better off hiding or using camouflage.

Future plans are to extend this model by increasing variation in environmental disturbances and behavioural reactions of the foragers, to investigate how far the basic competences used in this study will suffice, or what levels of animal cognition become necessary in order to cope with more variation in the environment.

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CRediT authorship contribution statement

J. Fransje van Weerden: Conceptualization, Software, Visualization, Writing - original draft. **Rineke Verbrugge:** Conceptualization, Writing - review & editing, Supervision. **Charlotte K. Hemelrijk:** Conceptualization, Writing - review & editing, Supervision.

Declarations of Competing Interest

None.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.ecolmodel.2020.109073.

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