Title:

Flash Expansion and the Repulsive Herd

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TITLE

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ABSTRACT

The Selfish Herd hypothesis, as proposed by Hamilton in 1971, is a powerful hypothesis to explain emergent grouping behaviour by individuals acting in their own self-interest. However, immediately after prey detect a predator, the prey group may undergo a rapid disassembly, called a flash expansion, which might be considered a “repulsive herd”. Although flash expansion occurs in bird flocks, fish schools, and insect swarms, few empirical or simulation studies have directly examined it or tested if there are differences among its members. Additionally, flash expansion is typically thought of as a near-simultaneous movement of individuals away from the group centre, little data has been collected to verify this. We performed an empirical study to test whether the overall movement of individuals within a flash expansion is away from the 1) first individual to startle; 2) geometric centre; or 3) point of highest density. Replicate swarms of marked whirligig beetles (Gyrinidae: *Dineutes*) were videotaped during flash expansion and their trajectories determined. Overall, individuals were found to move away from the geometric centre, more strongly than for the density maximum or the first to respond (starter). The geometric centre hypothesis was also supported by the lack of polarization of the group and that the bearing angle was away from the geometric centre. It was found that the starter was more likely to be a female at the edge of a group and that she moved more quickly than others and favoured the centre of the group. This is one of the first detailed examinations of flash expansion and the individual differences within it. Future empirical and simulation studies of the movement rules and emergent properties of flash expansion are needed to better understand the collective motion of other animals.

Keywords:

Flash Expansion, Propagation Wave, Collective motion, Selfish Herd, grouping, Dineutes, Whirligig, Swarm

INTRODUCTION

The Selfish Herd hypothesis (Hamilton, 1971) is a powerful concept which predicts that animals acting in their own self-interest can produce an emergent group. Thousands of papers (2500+) have cited this seminal work concerning proximate and ultimate factors effecting grouping and centripetal forces (Krause & Ruxton, 2002). According to this hypothesis, if a predator can appear anywhere within the group, each individual's best move is to reduce its domain of danger by moving towards its nearest neighbour. Later refinements to the model suggest that it is better to minimize approach time (Krause & Tegeder, 1994) or to go between one's two nearest neighbours (Morton, Haefner, Nugala, Decino, & Mendes, 1994) or that edge and center individuals may have different optimal movement rules to achieve reduced domains of danger (Morrell, Ruxton, & James, 2011).. However, little is known about the opposite "repulsive" centrifugal forces. We refer specifically to the emergent group behaviour called flash expansion (**FE**), defined (but not confirmed) as a near simultaneous movement away from the group during the final "attack" phase of a predator strike (Magurran & Pitcher, 1987; Parrish & Pitcher, 1997; Partridge, 1982). FE is thought to reduce a predator's capture rate by confusing it (Partridge, 1982). There are a number of unanswered questions about the FE such as do individual differences in sex, hunger, and boldness have an equal likelihood of being in the centre or edge of groups at different phases of the FE and does the individual who sees the predator first behave differently from other group members? It is also unclear how an FE compares with the better-studied propagation waves (Procaccini et al., 2011).

There are few detailed studies of FE. In fish, the FE is typically the very last school response to a predator after other escape behaviours have been exhausted (Magurran & Pitcher, 1987). Many species of fish exhibit an FE which starts with a reflex “C-start” (a fast startle response) followed by movement away from the group (Parrish & Pitcher, 1997). For fish, it has not been shown whether the individual trajectories move directly away from the starter, from the group centroid, or some other reference point. Additionally, the signal modalities in fish may be sound, pressure waves (perceived by the lateral line system), chemical signals, or visual cues. Therefore, many possible mechanisms exist by which fish may receive threat signals, which makes studying FE in these animals difficult.

Because fish make such a complicated model, it may be more practical to study the FE phenomenon in other animal taxa, and indeed, this has been done several times. For example, the trajectories of stationary midge and mosquitoes swarms have been well characterized (Diabaté et al., 2009; Goldsmith & Okubo, 1980; Kelley & Ouellette, 2013; Manoukis et al., 2009), but their FE has not. In birds, one would expect there to be distinct differences between the FE of a flock initially resting on the ground (or water) vs. one that is already airborne (Davis, 1975; Roberts, 1997). Only a few simulation studies have addressed FE. One of these is a paper in which a simulated predator is introduced into a group (Couzin & Krause, 2003) and the other addresses the success of a predator’s repeated attacks on a group (Lett, Semeria, Thiebault, & Tremblay, 2014). However, these are simulation studies; so far as we know, no empirical studies demonstrating FE have been reported for birds.

Another emergent response in groups, the escape/propagation wave, , has been better studied than FE. Studies on insects, fish, and birds have documented internal waves which spread across the group starting from the side which was first disturbed (Herbert-Read, Buhl, Hu, Ward, & Sumpter, 2014; Procaccini et al., 2011; Treherne & Foster, 1981). These density waves move faster than the individual and are thought to propagate information as a

“contagion” through the group (Rosenthal, Twomey, Hartnett, Wu, & Couzin, 2015). One way of testing whether an internal wave exists in a group is to measure the polarization and density at different parts of the group over time (Procaccini et al., 2011). Escape wave development can be divided into three phases (Lima, 1995; Quinn & Cresswell, 2005). First, the early detectors respond to the stimulus. Next, the nearby non-detectors respond. Finally, the whole group moves.

The above studies suggest that each individual group member may respond to an attack in a different way. Consequently, we categorized individual response in addition to group response. We operationally defined “**starter**” as the first individuals in a group to respond and “**followers**” as the rest of the group. Other authors use alternative terms such as: “knowledgeable/naïve” (Mirabet et al., 2008; Stienessen and Parrish, 2013) or “early/late responders” (Marras & Domenici, 2013). Even though we use the term “follower” in this paper, these individuals may just be those that notice the predator later, and are not following the starter at all. For the ones that do, the starter may transmit information to the followers inadvertently or as a purposeful signal (alarm call) (Quinn & Cresswell, 2005). The relationship between the starter and the follower can be described as either altruistic, cooperative, or manipulative (Sherman, 1985). Goulart and Young (2013) found that after a predator exposure, some fish are manipulative; they harass conspecifics in their school so that the predator notices them first.

The relationship between escape waves and FE is not clear, and will be examined in this study. It is possible that propagation waves and FE are both emergent properties of the same attraction/repulsion movement rules, but under different circumstances. Alternatively, it is possible that they are fundamentally different and serve different functions, i.e. the FE may be an adaptive coordinated group response to confuse the predator, whereas a propagation wave may be a non-adaptive by-product (Camazine et al., 2001) of individually adaptive

movement rules. Perhaps the difference between FE and escape waves has to do with the starting group size and density (with FE occurring in smaller, denser, groups).

The study organism for this paper is the whirligig beetle (Gyrinidae: *Dineutes discolor*). These beetles are ideal model organisms because they can be brought into the laboratory, individually marked, analysed in 2-dimensions, and readily stimulated to produce a flash expansion (Romey, 1995). They are aquatic beetles whose adults swim at the surface of the water eating insect detritus and avoiding a variety of predators which attack from above and below (Heinrich & Vogt, 1980; Vulinec & Miller, 1989). Whirligig beetles are unusual among insects in that they group primarily to avoid predators, not for reproduction. Nor do they group in family units, as do bees and ants, which would complicate the “selfish” grouping explanations. Individual differences within whirligig swarms have been well characterized. Within resting groups, individuals occupy different positions according to hunger, sex, and perceived threat, but not dominance hierarchy (Romey, 1995; Romey & LaBuda, 2010; Romey & Wallace, 2007). They have a variety of defensive mechanisms, including upward and downward pointing eyes, surface wave detecting antennae (Kolmes, 1983), and defensive chemicals (Eisner & Aneshansley, 2000). When startled by a visual stimulus, groups exhibit an FE, as characterized by an increase in the speed of individuals, outward expansion of the group for 1-2 seconds, then re-aggregate in the same location (Romey, Miller, & Vidal, 2014). Although there are fine-grained kinematic studies of individual whirligig beetles (Newhouse & Aiken, 1986; Tucker, 1969; Voise & Casas, 2009), few researchers have examined the trajectories of a group during an FE. A small number of sighted whirligigs, in a group that was otherwise blinded, were sufficient to initiate a flash expansion (Vulinec & Miller, 1989).

In this study we characterize the individual trajectories of swarms of whirligig beetles during FE. We measured the speed and turning rate of individuals over time and the distance

of beetles away from key reference points. We tested three hypotheses for the proximate mechanism of an FE: H1) individuals move away from each other in a way that overall movement is away from the area of initial highest density (a repulsive herd); H2) individuals move away from each other in a way which leads them away from the initial geometric centre; and H3) individuals move away from the first animal to accelerate in response to a predator. The first two hypotheses could arise as a result of local attraction and repulsion rules (Romey, 1996) rather than a direct knowledge of the group centroid or point of highest density. If H1 is true, then we predict that individuals would radiate away from different places within the group and the resulting group perimeter would be irregular. If H2 is true we predict that the average distance from the centre would increase more rapidly than from the densest location or from the first to startle. Also we would predict that individual bearing angles would be away from the geometric centre and the perimeter of the group would be relatively smooth. Last, if H3 is true, we predict that beetles would become more polarized as a density wave moved across the group. We also examined individual differences on movements of individuals during the FE. Specifically, we compared whether the first individual to move (starters) behaved significantly differently from the others and if there was a difference between the trajectories of males and females.

METHODS

Whirligig beetles (*Dineutes discolor*) were dip-netted in the Raquette River, Potsdam, New York, USA in July 2014. Whirligig beetles were stored at room temperature (21°C) in 100 cm diameter plastic stock tanks filled to a depth of 5 cm with aged tap water at the Biology Department, in the State University of New York at Potsdam. A light/dark cycle of 15:9 was maintained. Beetles were fed freeze-dried bloodworms (0.1 g/25 beetles) every morning and evening. Beetles acclimated indoors for at least 36 hours before filming. The sex

of beetles was determined using their front tarsus and 120 beetles were marked each week with 2 paint dots (Romey & Galbraith, 2008) on their elytra to denote sex. On alternate weeks the colour pattern was changed. After marking, beetles were kept in batches of 30 in 38-liter glass aquaria under these standard conditions. Each beetle was used no more than twice on a given day, never in the same group. At the end of testing, beetles were returned to the river.

A separate filming tank was surrounded by white curtains to reduce extraneous stimuli. Lighting in this tank was adjusted to provide 1200 lux at the water's surface using four 120 watt-equivalent compact fluorescent lights with a colour of 5000 Kelvin. In order to produce a consistent FE, a spoon-like fright stimulus was designed akin to Brown and Hatch (1929). They found that it is the rapid change of contrast, more than the motion itself of a predator, which triggers the fright display of whirligigs. Our display consisted of a 40 cm diameter disk (black on one side and white on the other) fixed to a rigid pole. It was suspended behind the camera (3 m away from insects) directly over the centre of the group with the white side facing the group initially. To stimulate an FE the handle was turned rapidly so that the black side of the disk was exposed almost instantaneously against the white ceiling. Since there was no horizontal movement and the stimulus was directly overhead, all of the beetles in the group (edge and centre) had an equal chance of seeing the stimulus. A Canon 60-D camera was centred over the middle of the tank 3 m below. Camera movie settings were set to: 1920 x 1080 resolution, 30 frames-per-second, 1/480 shutter speed, 3.5 f-stop, and 1250 ISO. A remote control was used to start the camera to avoid disturbing the beetles prematurely.

For a given trial, 30 whirligigs (15 marked males and 15 marked females) were assembled randomly from the treatment tanks and placed into the filming tank. In order to obtain a random sample the beetles were first disturbed, then a sweep net was drawn across the tank. Beetles were given a 1-2 hour acclimation period in the filming tank while

periodically (approximately every 15 minutes) disturbing them with a black flag to promote grouping. After the formation of a tight group the camera was started, the predator stimulus was given, and the next 30 seconds were recorded. Prior to FE, beetles move very slowly. After they see the stimulus, a “starter” beetle accelerates first then the rest of the group starts moving rapidly. We were always able to discern one beetle that was the first to start moving and cross-verified it with another observer on the rare case in which two began moving at about the same time. After one or two seconds the whole group reaches its maximum width and speed and continues for several more seconds until the group coalesces and slows.

Video segments were then converted from MXF to AVI format using Virtual Dub64. This footage was then imported into ImageJ (Rasband, 2004) and analysed with the MtrackJ plug-in (Meijering E, 2012). We analysed the tracks of beetles from the time when the starter accelerated to the time when the group was at a maximum width (typically about 40 video frames, or 1.3 seconds). The starting image, while the beetles were still resting, was analysed using ImageJ to determine group area and density. Three reference points were determined from this first video frame: the starter, the group centre, and the density-max. The position of the starter was determined when it first accelerated. This acceleration was seen as a small water wave. The group centre was calculated as the mean of the coordinates on the first frame of the video. The density-max was determined by placing a 1x1 cm grid over the video image and choosing the coordinates of the centre of the grid where the greatest number of whirligigs occurred (about 3-4 beetles).

Trajectories of each beetle were determined using MtrackJ. Each beetle was tracked from the start until FE reached its maximum width. Beetles more than 10 body lengths away from another beetle were not included in the analysis. This led to a mean group size of 22 (with a range of 19-25). The distance from the last point, heading, change in angle since last

vector, and the distance of each point away from the three reference points (starter, centre, and density-max) was then determined.

Time intervals were truncated at 36 frames and divided into seven equal intervals of 5 frames each (2-6, 7-11, etc.). Starting density (beetles/cm²) of the group was calculated by dividing the actual number of beetles in the group by the area within the minimum spanning polygon. The turning rate of an individual was calculated as the mean of the absolute value of the change in turn angle at every frame. Circular statistics to determine bearing angles and polarization (Rayleigh test for the uniformity of orientations and One-sample t-test for the mean angle) were performed using the CircStat toolbox for Matlab (Berens, 2009). To improve normality before applying statistics, the following transformations to the raw data were made: change in angle was natural log transformed; speed and the distances to the three reference points were square-root transformed. Generalized Linear Mixed Models (SPSS v. 22) were calculated on the transformed variables using “group(beetle)” as a random factor.

RESULTS

The trajectories of individuals in 13 groups of beetles were analysed (Fig. 1). They consisted of a mean of 22.4 individuals and a mean pre-FE starting area of 367.6 cm² (density = 0.069 beetles/cm²). The speed of the beetles increased rapidly at the start of the FE to approximately 1.5 cm/frame (45 cm/s), and then plateaued (Fig. 2). The average turn rate of the beetles was highest at the start of the FE then decreased steadily (Fig. 3). Followers (both males and females) moved away from the three reference points at about the same rate (slope) (Fig. 5, dashed lines). There were no significant differences between males and females in any of the results (Table 1, post hoc LSD, $P > 0.05$).

The starter beetles moved differently from the follower beetles in most of the measured variables (Fig. 5). LSD post-hoc tests showed that the starter was significantly different than male or female followers ($P < 0.05$), but there was no significant difference between the sexes of the followers. The starter was significantly more likely to be a female than male (11 vs. 2, $\chi^2 = 6.23$, $P = 0.012$). The starter beetle was significantly more likely to be on the outside of the group initially, but then to move quickly to the middle of the group (Fig. 5b). The interaction effect between type of individual (starter vs. followers) and time is significantly different in all of the measures (Table 1). The starter had a significantly faster speed than the others in a group (Figure 2, Table 1). The starter turned significantly less than the others in a group (Fig. 3, Table 1). The starter was also different from the others in the group in that it moved away from its starting point at a more rapid rate than others in the group (Fig. 5a). The distance of the starter from the density-max was significantly different than the rest of the group (Fig. 5c, Table 1).

To test whether the beetles were polarized and orientated towards a common direction, we performed a Rayleigh test on every frame with >10 orientation values. On the starting frame, 8/13 groups were polarized (significantly different from homogeneous) suggesting a tendency for the resting beetles to be aligned. After this first frame, polarization was uncommon; in all 13 groups, only 52/556 frames were significantly different ($P < 0.05$) from a homogeneous distribution indicating that the beetles' orientations were evenly spread.

To test whether beetles moved away from the initial position of the centre of the group, we calculated their bearing relative to this point (that is, the angle between the vector corresponding to the current velocity of the beetle and the vector joining the initial location of the centre of the group to the current location of the beetle). A value of zero degrees indicates that the beetle is moving away from the group centre while a value of ± 180 degrees corresponded to a movement directly towards the centre. The distributions of the bearings

relative to the centre of the group were significantly different from homogeneous most of the time (Rayleigh tests with $P < 0.05$ for 93.1% of the frames in the intervals 1-30). A closer look reveals that after an initial early phase during which the relative bearings were wide spread (Fig. 4a), they tended to gather around zero (with 70% of frames in the 21-30 interval (Fig. 4b) not being significantly different from a mean angle value of zero (Zar, 1999), that is directly away from the centre, while the distribution later on (Fig. 4c) was more bi-modal with peaks around ± 90 , possibly indicating a tendency for beetles to enter a milling movement instead of moving further away. The proportion of frames in which the mean angle was not different from zero changed from 33% to 30% to 70% during successive thirds of the FE.

DISCUSSION

The flash expansion manoeuvre in whirligig beetles occurs in less than a second and is characterized by a rapid increase in speed and a decrease in turning. Of the three hypotheses initially proposed to explain FE, our data best support H2, that the overall movement of whirligigs was away from the geometric centre, rather than away from the density maximum or from the first beetle to startle. For this hypothesis we had predicted that the distance away from the centre reference point would increase the most sharply, beetles would be unpolarized during most of the FE, and that their bearing angle would be oriented away from the centre. All three of these predictions were true for the majority of beetles (male and female followers). Although Fig. 5 shows that the distance away from all of the three reference points increases, a comparison of significance and F-values for the effect of Time in Table 1 shows that the distance to the centre has the strongest effect of the three. Interestingly, the mean bearing angles to the centre of the group (Fig. 4) show that beetles moved randomly at first then away from the centre.

Most of the predictions of H1 (the reverse Selfish Herd) were not supported. First, the strength of the relationship was stronger for the movement away from the geometric centre (H1) than the Density-Maximum (Table 1, p-values). We predicted unpolarized movement, for both H1 and H2 so we were not able to discern between hypotheses based on this finding alone. Finally, we predicted that H1 would lead to a more irregular group perimeter whereas H2 would be more circular. Qualitatively, we observed a very circular perimeter which supports H2 over H1. However, future more quantifiable studies of the perimeter before and after FE and using simulation models as comparisons would help to answer this question. So, it does not appear that we should call FEs in whirligig beetles a “repulsive herd”, although we do not yet know about other taxa.

H3 predicted that we would observe a density wave across the group starting with the first beetle to startle. We also predicted that we would find significant polarization for this hypothesis (if the first to startle was on the edge, not the middle), but not a unified bearing angle away from the geometric centre of the group. Also H3 predicted that the shape of the group would go from relatively round to a more elongated shape. These predictions were not supported by the data. As well as a lack of polarization, visual examination of the trajectories of the 13 FE (e.g. Fig. 1) did not show either a progression from one side of the group to the other. The first beetle to startle was usually on an edge. And, although there is an increase in the average distance of individuals from the starter’s initial position (Fig. 5a), there would be a general increase in distance from all of the individuals in a group as it expanded. The shape of the group remained circular (qualitatively) as the FE progressed rather than becoming more cigar-like. The FE that we observed appears to be a very different phenomenon than the propagation/escape wave recently studied in fish and bird groups (Herbert-Read et al., 2014; Procaccini et al., 2011).

The other main goal of this study was to examine if there were individual differences within the FE. This has never been examined in groups before. We found that the marked male and female followers did not differ from each other in any of our measured variables, but that the starter was significantly different from the rest of the group in speed, distance to the centre, and displacement from the original location. So, even though the rest of the group does not seem to react as a wave from the starter's initial position, the starter may stimulate the rest of the group to FE. The starter beetle's behaviour could be mutualistic in that all of the beetles benefit by a well-developed FE. Alternatively, the starter beetle's behaviour could be manipulative in reducing its own risk of predation, while increasing others. Goulart and Young (2013) documented such a strategy; a fish under attack by a predator attacks shoal-members to deflect attention away from itself. Marras and Domenici (2013) found that certain fish are more likely to startle first in response to a predator. It would be interesting to examine if this also occurs in whirligig beetles during FE. Previous research with whirligigs found that outer whirligigs are more likely to be hungry (Romey, 1995) and more likely to be the first to respond from a side-approaching predator (Romey et al., 2014). In the current study, care was taken to position the predator stimulus directly over the top of the group, so each group member would have an equal chance of seeing it. The starters may have a stronger motivation to avoid predators than the others, because they have certain knowledge that there is a predator, whereas follower beetles may be naïve and not want to react to a false alarm. Since the starter was knowledgeable about the existence of a predator, this could explain why it took up a position in the centre of the group in our study, after detecting the stimulus. Central positions have been found to be safer, even in two-dimensional groups like whirligigs (Romey, Walston, & Watt, 2008). It is unclear why the starter turned less than other group members in our empirical study.

One mechanism for the observation that individual members move away from the geometric mean of the group is that the starter may have moved there and stimulated others to move away from this area by its rapid movement. It is tempting to think of our results in terms of an alarm call such as seen in Belding's ground squirrels in which the informed individuals take up the safest position once they have made an alarm call and stimulated movement of the other animals (Sherman, 1985). However, additional finer-scale information would have to be collected to test that hypothesis and whether it was purposeful or passive communication. In a study of a school of fish (Stienessen & Parrish, 2013) it was shown that knowledgeable individuals, those that knew food was about to arrive, increased their speed, but stayed on the outside of the school where there would be more food. Our observation that the starters were more likely to be female than male may be due to differences in vigilance, or their perceived risk of predation. Our data showed that there was no significant difference in the distance to the centre between males and females (Fig 5b) although other studies (Romey & Wallace, 2007) show that, if anything, males are more likely to be on the outside of groups than females. In a variety of other taxa it has been found that females have higher vigilance levels than the males of a group (Rieucau et al., 2012).

Our findings suggest a variety of other empirical and simulation studies to better understand FE. In our study system, as well as others, it would be useful to systematically vary the group size and density of the starting group to see how that influences the response. For example, sticklebacks were found to attack the densest part of a group of *Daphnia*, but also to have a higher error rate (Ioannou et al., 2009). Also, as mentioned, it would be useful to see if some individuals were more likely to repeatedly startle (Marras & Domenici, 2013) and stimulate an FE and whether this was related to shy/bold behaviour or other behavioural syndromes (Sih, 2004). Simulation studies using individually based models (Couzin, Krause, Franks, & Levin, 2005; Romey & Vidal, 2013) would be helpful in differentiating between

these hypotheses. Furthermore, by using clever combinations of simulated individuals and real predators (Ioannou, Guttal, & Couzin, 2012) one could understand the adaptive value of occupying different parts of the group during a flash expansion. Future studies of FE would do well to analyse how individuals move away from the densest area in their local moving neighbourhood, more than just one densest part of the group at the beginning as we have done here. Future studies should also determine if FE is qualitatively the same as a polarized group wave or just two different emergent properties that are based on the same movement rules.

In conclusion, this is one of the first studies to closely examine the trajectory of animals during FE. This is an example of emergent group behaviour in which each animal may not know what the others are doing, yet there is an adaptive group response (Camazine et al., 2001). Despite the differences among birds, fish, and insects, we believe that there may be common movement rules during FE, brought about by convergent evolutionary pressures. We found that whirligigs move away from the geometric centre of the group, more than the area of maximum density or the initial position of the first beetle to startle. We also found that not all of the beetles respond in the same way to a predator attack during FE; the starter moved more quickly than others and moved from the outside to the centre of the group. From here, the starter beetle may have stimulated the rest of the group to action. Our findings here are important in establishing the preliminary analyses of FE in a representative species and should be repeated in more detail with a variety of insects, fish, and birds. Also, the concept of flash expansion may be important for understanding how groups of people or autonomous vehicles under attack might coordinate themselves (Helbing et al., 2000; Lin, Broucke, & Francis, 2004).

374 **Acknowledgements**

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Figure

Figure 1

Figure 2

Figure 3

Figure 4

Figure 5a

Figure 5b

Figure 5c