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Flash expansion and the repulsive herd

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The selfish herd hypothesis, as proposed by Hamilton (1971, *Journal of Theoretical Biology*, *31*, 295–311), 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 whether there are differences among its members. In addition, although 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 (1) the first individual to startle, (2) the geometric centre or (3) the point of highest density. We videotaped replicate swarms of marked whirligig beetles (Gyrinidae: *Dineutes*) during flash expansion and determined their trajectories. Overall, individuals moved away from the geometric centre more strongly than from 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. The starter was more likely to be a female at the edge of a group, and 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.

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 centre individuals may have different optimal movement rules to achieve reduced domaines 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, 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). Flash expansion is thought to reduce a predator's capture rate by confusing it (Partridge, 1982). There are a number of unanswered questions about flash expansion, such as do individual differences in sex, hunger and boldness have an equal likelihood of being in the centre or the edge of groups at different phases of the flash expansion and does the individual who sees the predator first behave differently from other group members? It is also unclear how flash expansions compare with the better-studied propagation waves (Procaccini et al., 2011).

There are few detailed studies of flash expansion. In fish, the flash expansion 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 a flash expansion, which starts with a reflex 'C-start' (a fast startle response), followed by movement away from the group (Parrish &

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Pitcher, 1997). For fish, it has not been shown whether the individual trajectories move directly away from the starter, from the group centroid, or from some other reference point. In addition, 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 flash expansion in these animals difficult.

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

Another emergent response in groups, the escape/propagation wave, has been better studied than flash expansion. Studies on insects, fish and birds have documented internal waves that spread across the group starting from the side that 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 nondetectors 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 & 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 flash expansion is not clear, and will be examined in this study. It is possible that propagation waves and flash expansion 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; that is, the flash expansion may be an adaptive coordinated group response to confuse the predator, whereas a propagation wave may be a nonadaptive by-product (Camazine et al., 2001) of individually adaptive movement rules. Perhaps the difference between flash expansion and escape waves has to do with the starting group size and density (with flash expansion 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 two 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 that 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 a flash expansion, as characterized by an increase in the speed of individuals, outward expansion of the group for 1–2 s, then reaggregation 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, 2010), few researchers have examined the trajectories of a group during a flash expansion. 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 flash expansion. We measured individuals' speed and turning rate over time and their distance away from key reference points. We tested three hypotheses for the proximate mechanism of a flash expansion: (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 that 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 from direct knowledge of the group centroid or the point of highest density. If H1 is true, then we predicted that individuals would radiate away from different places within the group and the resulting group perimeter would be irregular. If H2 is true, we predicted that individuals' average distance from the centre would increase more rapidly than their average distance from the densest location or than their average distance from the first to startle. We also predicted that individual bearing angles would be away from the geometric centre and that the perimeter of the group would be relatively smooth. Last, if H3 is true, we predicted 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 flash expansion. Specifically, we compared whether the first individual to move (starters) behaved significantly differently from the others and whether there was a difference between the trajectories of males and females.