



Is the quorum threshold for emergent group response in whirligigs absolute or proportional?

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Groups of animals sometimes coordinate their individual behaviours to produce an emergent group response. Examples of these quorum responses include stampedes in ungulates and orientation flights in honeybee swarms. In these groups, there may be some individuals who are knowledgeable about the threat or direction to go to, and others who are not. Few experimental studies have convincingly addressed whether the number of knowledgeable individuals to trigger an emergent group response is a fixed (absolute) number or a fixed proportion (percentage) of the group. We tested whether this threshold to produce an emergent group response was absolute or proportional in an experimental study of whirligig beetles (Gyrinidae: *Dineutes*). When whirligig beetles see an aerial predator, individuals make a startle response. If enough beetles startle, then the whole group makes a flash expansion. In our study, we manipulated the numbers of beetles in a group that were able to see the predator model by covering their eyes. We also manipulated group size (12, 24, 48). Our results reject the absolute hypothesis and support the proportional hypothesis for how many knowledgeable whirligigs it takes in a group to elicit an emergent flash expansion. At all three group sizes the threshold was approximately 10%. We also examined the interaction of the ratio of sighted/unsighted beetles and group size on swarm density, group area and longevity (duration of the flash expansion). Longevity was significantly leptokurtic, as would be expected for a stereotyped display. This is one of the first controlled empirical studies to differentiate between absolute and proportional thresholds in producing an emergent predator avoidance response.

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Emergent properties of groups arise from the movement rules of individuals (Krause & Ruxton, 2002; Romey & Lamb, 2015; Romey, Smith, & Buhl, 2015; Ward, Herbert-Read, Sumpter, & Krause, 2011). Individual differences in hunger, gender, knowledge of food sites and predators influence how an individual moves within the group and influences the movement of others in that group (Dyer, et al., 2008; Krause, 1993b; Romey, 1996). There is a lack of data in the literature on whether emergent group movement is triggered by an absolute number of individuals (regardless of group size) or whether it is triggered by a proportion of the group. If the members of a group are closely related, as they are in eusocial hymenoptera, then the movement of a few individuals may indicate an honest signal. For example, one honeybee can trigger an alarm response in a whole swarm by releasing a pheromone, or 5% of the honeybees in a swarm can steer a group to a new nest site (Seeley & Buhrman, 1999). However, in groups of unrelated individuals, there may be

conflicting evolutionary motives wherein the fitness of the signaller differs from the fitness of others (e.g. 'selfish herd'; Hamilton, 1971). For example, one individual may cause a startle display that reduces its own predator risk but increases the risk to others in its group (Sherman, 1985). Therefore, the number of informed individuals may need to reach a higher threshold in unrelated groups of animals before a group consensus forms and an emergent group response occurs (Conradt, Krause, Couzin, & Roper, 2009; Conradt & Roper, 2005; Couzin et al., 2011; Couzin, Krause, Franks, & Levin, 2005). These emergent group responses, also known as quorum responses, have been much studied recently (Sumpter & Pratt, 2009; Walker, King, McNutt, & Jordan, 2017; Ward, Krause, & Sumpter, 2012).

Some studies suggest absolute thresholds for emergent group behaviour (foraging and predator avoidance behaviour for example) but do not explicitly examine variation in group size. Field studies of mammals sometimes do not have the range in group sizes to differentiate between the absolute and proportional hypothesis. In a recent paper on African wild dogs, *Lycaon pictus*, Walker et al. (2017) found that it took about three individuals in an average group size of nine to trigger the group to move to a new

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area (associated with a novel sneezing signal). Similarly, the threshold for a group of meerkats, *Suricata suricatta*, to move is three individuals in an average group size of 11 (Bousquet, Sumpster, & Manser, 2011). In hierarchical groups such as this, with a relatively constant group size, the question of absolute versus proportional thresholds is less of an issue than in fission–fusion groups such as insect swarms, fish schools and bird flocks. In a study of fish schools of a single group size, it took 1 in 12 knowledgeable fish to lead a school to a food patch (Reebs, 2000). Stienessen and Parrish (2013) found that a threshold of 20% (at a single group size) of knowledgeable fish had to be reached before an emergent school-feeding response took place. And in a simulation model, Couzin et al. (2005) found an absolute number of 5–10 individuals was enough to steer groups of many different sizes. The threshold also seems to be an absolute number in alarm-calling behaviour such as in honeybees (Seeley & Buhrman, 1999), ground squirrels (Sherman, 1985) and fish (Krause, 1993a). This low absolute threshold to sound an alarm may be because individuals are closely related and there is a reduced incidence of false alarms (Beauchamp, 2010).

Only a few empirical studies have examined the influence of group size on thresholds for emergent group behaviour. In a field study of undisturbed sanderlings, *Calidris alba*, a consistent proportion of birds (about 11%) had to leave the group before the whole flock took to flight in groups ranging in size from 2–120 (Roberts, 1997).

The emergent group response of interest in the present study is the flash expansion of whirligig beetles (Gyrinidae). A flash expansion is a stereotyped predator avoidance response in which grouped animals move quickly away from each other, maintain this speed while circling and staying together as a group, then slowing down and regrouping in approximately the same location as before (Magurran & Pitcher, 1987; Parrish & Pitcher, 1997; Romey & Lamb, 2015). The adaptive function of a flash expansion is presumably the confusion effect, making it difficult for a predator to target one individual (Parrish & Pitcher, 1997). Whirligig beetles were used in this experiment because they are easily manipulated and filmed in the laboratory and produce flash expansions that are very much like those seen in fish and birds. Also like many schools and flocks, whirligig swarms are composed of unrelated individuals, unlike hymenopteran groups. Whirligig beetles are aquatic insects that swim at the surface of the water during the summer. They eat insects trapped at the water's surface and have predators that attack them from above, below and laterally. Some of their special adaptations for avoiding predators include grouping, sensitive dorsal and ventral eyes, paddle-like feet and defensive chemicals (Heinrich & Vogt, 1980). Vulinec and Miller (1989) found that if 50% of beetles were temporarily blinded a full group response did not occur in response to visual disturbances. In a previous experiment with a single group size (24), we found that a threshold of four knowledgeable beetles (16%) was needed to produce an emergent flash expansion response (Romey & Lamb, 2015). In another study, we found that whirligigs primarily use vision to detect predators whereas the flash expansion response is coordinated by antennal responses to surface waves on the water (Romey, Miller, & Vidal, 2014).

We tested two hypotheses in this study, the absolute number hypothesis and the proportion hypothesis. The absolute number hypothesis states that a fixed number of individuals must react to cause a group response. If this hypothesis is correct, then we predicted that the same number of individuals would be needed to cause a response, regardless of group size. In contrast, the proportion hypothesis states that a percentage of a group must react to cause a group response. If this hypothesis is correct, then we predicted that the number of individuals needed to cause a response would increase linearly with group size. To test these two

hypotheses we obstructed the eyes of different proportions of beetles in replicated groups to manipulate absolute numbers and percentages of knowledgeable individuals at different designated group sizes (12, 24, or 48). We then presented a standardized predator stimulus model to the group and measured the emergent response, especially whether it was a partial group response or a full flash expansion. We then distinguished whether the number of whirligig beetles to trigger a full flash expansion was a fixed number (absolute) or a consistent proportion of beetles at all group sizes.

METHODS

Whirligig beetles (Gyrinidae, *Dineutes discolor*) were obtained weekly from the Grass River in Canton, NY, U.S.A. (44°35'51"N, 75°10'16"W) beginning on 24 August 2015. Whirligig beetles are very common in this area and occur in groups ranging in size from 10 to 5000. Approximately 150 beetles were captured each week with dip-nets then maintained in 20 °C stock tanks at the State University of New York at Potsdam. Collection and possession of the beetles was covered by New York State Department of Environmental Conservation Permit Number 1353. In the laboratory, we dipped a sweepnet into the tank and alternatively designated individuals into two categories: 'unsighted' and 'sighted'. For the unsighted beetles, we first marked their elytra with a colour dot of fast-drying oil paint (Faber-Castell PaintPen, <http://www.fabercastell.com/>). Then we carefully painted over their dorsal eyes with opaque black paint (following methods of Romey & Lamb, 2015). Their ventral eyes were left unobstructed so that they could see underwater but not the predator stimulus above the tank. Pilot studies composed of groups of 100% unsighted beetles did not respond at all to the overhead predator stimulus. The specific colour of the elytra paint dot was changed weekly for different groups to control for unintentional responses to the colour. For the sighted beetles, we marked them with a different colour on their elytra and handled them for about the same amount of time as the others, but did not paint over their eyes.

We kept the beetles in eight aerated 40-litre 'treatment tanks' with a stocking density of 15 beetles/tank. We gave beetles 2 days to acclimate to the laboratory and the manipulation before starting observations. Throughout the experiment, we fed each beetle 4 mg of freeze-dried bloodworms per day divided into a morning and evening feeding (the unsighted beetles were able to feed at the same rate as the sighted ones because feeding is mediated by touch rather than vision). We changed the water in the treatment tanks every 2 days and weekly in the experimental tanks. Treatment tanks were illuminated with two 60 W incandescent bulbs on a 13:11 h light:dark timer to simulate their normal photoperiod. At the end of each week, we returned beetles to the river and captured new ones. Returned beetles rejoin groups and are able to feed normally. Previous experience shows that the paint on their eyes wears off after about 10 days.

After acclimation, we assembled specific ratios of sighted and unsighted beetles into an experimental tank for filming. The experimental tank was a 1 m diameter plastic pool filled to a depth of 8 cm with aged tap water. We surrounded the tank with a white curtain so that the camera operator did not influence the beetles inadvertently. We illuminated the experimental tank indirectly using two 105 W compact fluorescent lamps (5000 K) on the ground that led to 310 lm at the water's surface. We filmed the beetles from a ceiling-mounted Canon 60D camera, 1.75 m from the pool, operating at 30 frames/s, 2500 ISO, 1/400 s speed, 5.6 aperture and 1920 × 1080 pixel resolution.

To produce a consistent predator stimulus we suspended a 0.55 m diameter disk 2 m over the beetles. The disk was white on

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