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Swarm intelligence in fish? The difficulty in demonstrating distributed and self-organised collective intelligence in (some) animal groups

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ABSTRACT

Larger groups often have a greater ability to solve cognitive tasks compared to smaller ones or lone individuals. This is well established in social insects, navigating flocks of birds, and in groups of prey collectively vigilant for predators. Research in social insects has convincingly shown that improved cognitive performance can arise from self-organised local interactions between individuals that integrates their contributions, often referred to as swarm intelligence. This emergent collective intelligence has gained in popularity and been directly applied to groups of other animals, including fish. Despite being a likely mechanism at least partially explaining group performance in vertebrates, I argue here that other possible explanations are rarely ruled out in empirical studies. Hence, evidence for self-organised collective (or 'swarm') intelligence in fish is not as strong as it would first appear. These other explanations, the 'pool-of-competence' and the greater cognitive ability of individuals when in larger groups, are also reviewed. Also discussed is why improved group performance in general may be less often observed in animals such as shoaling fish compared to social insects. This review intends to highlight the difficulties in exploring collective intelligence in animal groups, ideally leading to further empirical work to illuminate these issues.

Contents

1. Introduction: the mechanisms for improved performance in groups

A major benefit animals derive from social interactions is access to information (Dall et al., 2005; Danchin et al., 2004). This social information is relatively low cost as it does not require direct sampling of the environment (unlike personal or 'private' information, which can be costly), and the formation and maintenance of groups allows access to social information from more individuals for longer periods of time. The flow of information can be uneven, for example from particular individuals who have had relevant experience such as finding a rich food patch, or be more egalitarian where all group members have an even probability of detecting an approaching predator and all other individuals copy the anti-predatory response of the individual who by chance made the detection. With this shar-

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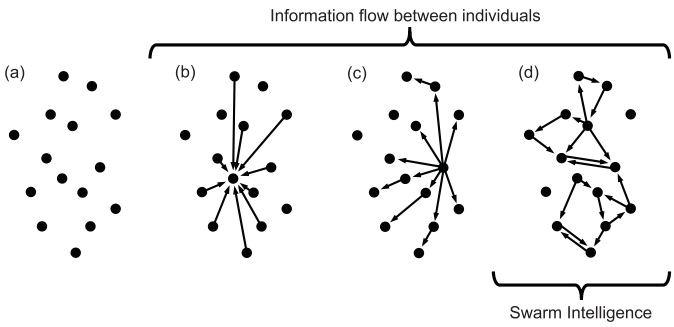

Fig. 1. Ways in which individuals in larger groups can make better decisions than individuals or smaller groups. Individuals are represented by circles, and the flow of information by arrows from the source to the recipient. (a) When there is individual-level improvement of cognitive ability, there is no flow of information between individuals. Instead, being in a group reduces the perception of predation risk, allowing individuals to allocate more cognitive resources into other tasks, or vigilance for predators where risk is not (or less) affected by prey group size. (b) Information can be centralised from all or some group members, where it is processed and either an overall group decision is made, or the information is made available to group members to use. (c) In the case of leadership, information flows from a single (or a few) individual(s) with pertinent knowledge to other group members. (d) Only in swarm intelligence is there information flow and no obvious key individual that centralises or leads. Note that for illustration, (a–d) show extreme cases. In the case of house-hunting ants for example, swarm intelligence occurs via self-organised interactions between scout ants (as in (d), but which are only a subset of the whole colony), and once a decision is made, the rest of the colony is led (c) by these individuals to the new nest site (Franks et al., 2003). Similarly, these processes are not mutually exclusive even at the same time. In a foraging group of birds (Morand-Ferron and Quinn, 2011), for example, individuals may have improved foraging due to a reduced perception of risk (a) and also benefit from the vigilant individual who detected the threat (c). In fish shoals, interactions occur directly between individuals (Ioannou et al., 2011), while in social insects they can be direct, for example resulting in lane formation (Fourcassié et al., 2010; Perna et al., 2012), or indirect, as occurs in trail formation via the deposition of pheromones (Moussaid et al., 2009).

ing of information, cognitive performance in ecologically relevant tasks such as predator avoidance and foraging can be improved for individuals and/or the group as a whole.

There are diverse ways by which improved intelligence via group behaviour can be achieved: there can be statistical aggregation of multiple opinions by a centralised agent (Galton, 1907), a reliance on a knowledgeable or motivated minority of the group leading others (Ioannou et al., 2015), or the decentralised decision making most commonly seen in social insect colonies (Bonabeau et al., 1999; Camazine et al., 2001) and slime moulds (Boisseau et al., 2016; Reid et al., 2016). Although the terms 'swarm' and 'collective' intelligence have been sometimes used to describe all of these mechanisms (e.g. Krause et al., 2009), here it is useful to explicitly define swarm intelligence as only improved cognitive performance in groups that arises from distributed, self-organised decision making (Bonabeau et al., 1999; Garnier et al., 2007; Kennedy et al., 2001; Reid and Latty, 2016). In this case, the critical factor is that the improved performance is primarily due to information being exchanged via repeated local interactions between individuals without any supervision of the process or centralisation of information (Fig. 1). The resulting network of interactions that arises during swarm intelligence is thus much more complex than in cases of leadership and centralising of information (Fig. 1). It is this relative complexity compared to other mechanisms (Fig. 1), resembling a seemingly disorganised but cohesive swarm of insects, that puts the 'swarm' in swarm intelligence (Kennedy et al., 2001).

Under these definitions, statistical averaging of many guesses can give accurate decisions in some tasks due to the cancelling out of noisy individual estimates (often referred to as the "wisdom of crowds"; Krause et al., 2009) and hence can be considered a mechanism that improves cognitive performance in groups through (albeit simple) interactions between individuals (e.g. Galton, 1907; Krause et al., 2009). However, its reliance on centralising information where it is processed (Fig. 1b) would exclude it from swarm intelligence. In contrast, in the 'many-wrongs' principle the noisy and inaccurate estimates of individuals in which direction to travel are cancelled out through a process of self-organisation (Codling et al., 2007; Simons, 2004). Here, individuals' direction of travel are influenced by both their private information (their opinion or preference to move in a desired direction) and the direction of travel of neighbours (Codling and Bode, 2016). While this can still be considered a form of averaging, it occurs at a local scale and there is a decentralised exchange of information as individuals are both influenced by, and influence, their neighbours (Fig. 1d). Importantly, improved performance in decision making from swarm intelligence arises as an emergent property of individual contributions and the interactions between individuals (i.e. the whole is greater than the sum of its parts). This makes performance through swarm intelligence much less predictable than via other mechanisms, and often requires computer simulations, as well as empirical work, to understand fully (Bonabeau et al., 1999).

To further illustrate the distinction between swarm intelligence and other mechanisms that result in better cognitive performance of groups, consider collective vigilance for predators. Here, groups have a greater ability to detect predators due to pooled vigilance (Elgar, 1989; Godin et al., 1988; Magurran et al., 1985; Taraborelli et al., 2012), often referred to as the 'many-eyes' effect. This is an example of group intelligence familiar to anyone who has taken an undergraduate course in animal behaviour, and is probably the earliest example of groups providing a cognitive benefit in non-human vertebrates to be documented (e.g. Miller, 1922). With more individuals in a group, there is a greater chance a predator will be detected, with this information being transferred to others in the group via intentional, active signals (Seyfarth et al., 1980) or passively from individuals copying fright or fleeing responses (Treherne and Foster, 1981). Although the transmission of information can occur at a local scale, and with individuals responding to the potential threat only via others that also did not directly respond (Herbert-Read et al., 2015), the flow of information can radiate out directly from a single responding individual (who acts as a temporary leader: Fig. 1c). Alternatively, there can be a more complex exchange of information between individuals, for example there may be feedback of information between individuals before they decide whether to respond (Fig. 1d). In both cases, there is an improvement in predator avoidance in larger groups as vigilance is distributed between many eyes, but whether it can be referred to as swarm intelligence according to the above definition will depend on how information subsequently flows between individuals. This is likely to vary between species, contexts, and with group size. Another issue is that there is a spectrum of interaction networks ranging from the simple (Fig. 1b, c) to the complex (Fig. 1d), and it is not clear at what level of complexity an improved decision by a group should be attributed to swarm intelligence. For example, if individuals require a cue from a threshold number of other individuals before responding themselves, as in quorum decision making (Sumpter and Pratt, 2009), but there is no bidirectional exchange of information between individuals, should it count as swarm intelligence?

Improved cognitive ability in larger fish shoals has been known for some time. Evidence suggests it is a taxonomically widespread phenomenon and occurs in a range of ecologically relevant contexts, including vigilance for predators (Godin et al., 1988; Magurran et al., 1985; Ward et al., 2011), foraging (Day et al., 2001; Pitcher et al., 1982; Smith and Warburton, 1992) and avoidance of pollutants (Hall Jr et al., 1982; McNicol et al., 1996). When observing a large, densely packed school of fish responding dynamically to avoid attacks from predators (e.g. Handegard et al., 2012; Magurran and Pitcher, 1987), it is hard to believe that

such responses are not a result of self-organisation and hence an example of swarm intelligence. However, the case for swarm intelligence in fish, defined in a strict sense where the improvement in cognitive performance comes from the integration of information from multiple individuals via self-organised local interactions, is maybe not as well established experimentally as it may first appear. While self-organisation in fish shoals is not in doubt (Hemelrijk and Hildenbrandt, 2012; Ioannou et al., 2011; Parrish et al., 2002), there are few studies that show better performance in a cognitive task in larger shoals and also demonstrate that the mechanism is based on self-organisation. In this review, I will argue it is actually quite difficult to rule out other explanations for improved performance in larger groups, and suggest possible avenues for future work to determine more clearly the mechanisms underlying improved cognitive performance in fish shoals. Part of the motivation for the review is a tendency for studies to usually favour one mechanism over others, while below I suggest instead that multiple mechanisms are likely to be operating simultaneously in many real animal groups (Morand-Ferron and Quinn, 2011). The review aims to bring together what is known about improved cognitive performance in groups of fish with other relevant aspects of fish behaviour to highlight outstanding issues and encourage further work to solve these issues in the future. Where relevant, I will draw on the literature in non-fish species, particularly social insects and birds, where a lot of previous work has been published on group performance in cognitive tasks (although often not referred to as collective or swarm intelligence). Similarly, although the focus is on fish, many of the issues I highlight will apply to other animals.

2. How could fish shoals achieve swarm intelligence?

As discussed above, the key to determining the underlying mechanism for improved cognition in larger groups is to understand the network of information transfer between individuals. In a diverse range of collectives, such as neural systems (Couzin, 2009), slime moulds (Reid and Latty, 2016) and social insects (Wilson and Hölldobler, 2009), the networks of how information is transferred and decisions ultimately made are relatively clear and easily mapped, allowing researchers to demonstrate distributed and self-organised decision making. In fish shoals and other types of groups like bird flocks, the cues that transfer information within groups are less clearly observed. Although group behaviour in animals has been studied for many decades (Krause and Ruxton, 2002; Ward and Webster, 2016), only recently have advances in computer vision tracking of animals from video and lightweight GPS units allowed high resolution data to be obtained from multiple individuals in a group simultaneously (Attanasi et al., 2014; Perez-Escudero et al., 2014; Pettit et al., 2015). These advances are now allowing models for how fish shoals and bird flocks form, move and make decisions (Aoki, 1982; Gautrais et al., 2008; Hemelrijk and Hildenbrandt, 2012) to be tested with real animals, allowing the networks of information transfer to be determined (e.g. Attanasi et al., 2014; Strandburg-Peshkin et al., 2013).

There are a diverse range of ways in which fish communicate actively with signals including sound (Ladich, 2000), body gesture signals (Godin, 1995), and colour change (Nilsson Sköld et al., 2013), particularly in the context of reproductive behaviour. However, our current understanding is that in the vast majority of shoaling fish, group formation, maintenance and information transfer occur through passive cues where each individual responds to the position and movement of near neighbours, the basic principle underlying models of collective motion. It is generally believed that fish primarily use two sensory modalities to achieve this (Ioannou et al., 2011): vision mediates attraction and alignment between individuals (Kowalko et al., 2013), while the mechanosensory lateral line, a shorter-range modality that allows fish to detect water movements, is believed to regulate repulsion so that individuals can avoid getting too close (Burgess and Shaw, 1981; Faucher et al., 2010), and allows fish to respond to rapid changes in the movement of neighbours as occurs during a startle response (Partridge and Pitcher, 1980). Importantly, cues from motion are relatively short range, limiting the extent of global cues (especially in larger shoals) that could transfer information from a single individual to all others directly. Thus, information transfer occurs locally, and increases the chance that information flows between individuals in complex ways (Fig. 1d), potentially allowing for swarm intelligence to emerge.

From an empirical perspective, this relatively simple form of information transfer has advantages. Using automated computer tracking from video (e.g. Delcourt et al., 2013; Perez-Escudero et al., 2014), the changes in movement of individuals in response to environmental and social cues can be quantified in detail, allowing researchers to determine how fish balance these sources of information in deciding where to move next (Berdahl et al., 2013; Strandburg-Peshkin et al., 2013). Further technology to record sound production or colour change of individuals (for example) does not seem to be necessary. It also allows manipulation through the use of robotic fish (e.g. Faria et al., 2010), which can be used to experimentally manipulate individual fish or shoals. For example, individual robot fish can be used to initiate fright responses to examine whether and how information spreads through shoals, or as a conspecific for a focal individual that will maintain shoal cohesion but not contribute to a cognitive task, such as detecting food or a predator.

A disadvantage however to having to track and quantify individual movements is that this is difficult in the field, which is especially true when filming underwater where visibility is restricted compared to in air. Thus a lot of work on group performance in fish has been limited to the laboratory by testing fish on a high-contrast background to facilitate observation and tracking, and the ecological validity of such studies not conducted in the wild remains unknown (Morand-Ferron and Quinn, 2011). While tracking of fish movements is possible from sonar, it has yet to be used to demonstrate collective intelligence under field conditions, although the responses of prey shoals to predatory attacks are likely to be a fruitful area of future research. For example, Handegard et al. (2012) used high resolution 'acoustic video' sonar to track movement in schools of juvenile Gulf menhaden (*Brevoortia patronus*) while being attacked by spotted sea trout (*Cynoscion nebulosus*). In this study, we showed that the distance over which information transferred in a group increased with group size, suggesting that more individuals have access to socially derived information in larger groups, which would help facilitate predator avoidance.

The relative ease with which aspects of fish sensory systems can be measured (e.g. Kowalko et al., 2013; Pita et al., 2015) gives great potential for testing how the information transfer driving swarm intelligence is in turn determined by sensory systems. This is especially true with new models of collective movement and collective detection of predators that make more realistic assumptions about the sensory properties of animals (Lemasson et al., 2013; Rountree and Sedberry, 2009), an approach which is supported by older experimental work in fish (Hunter, 1969). The study of Pita et al. (2015), for example, measured the field-of-view and visual acuity of two species commonly used to study collective behaviour, zebrafish (*Danio rerio*) and the golden shiner (*Notemigonus crysoleucas*). This was then used to make quantitative predictions for the improvement of collective detection of predators as a function of nearest neighbour distance, which showed that the potential for improved detection was greater in zebrafish compared to golden shiners.

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Table 1
Summary of studies using fish that have demonstrated an improved performance in a cognitive task in larger shoals and proposed a mechanism. Studies are given in the order they are discussed in the main text.

Refs.	Species	Proposed mechanism
Smith and Warburton (1992)	Blue-green chromis (*Chromis viridis*)	Individual-level improvement
Sumpter et al. (2008)	Three-spined sticklebacks (*Gasterosteus aculeatus*)	Swarm intelligence (quorum decision making)
Ward et al. (2011)	Mosquitofish (*Gambusia holbrooki*)	Swarm intelligence
Pitcher et al. (1982)	Goldfish (*Carassius auratus*) and minnows (*Phoxinus phoxinus*)	Not pool-of-competence
Berdahl et al. (2013)	Golden shiners (*Notemigonus crysoleucas*)	Swarm intelligence
Bisazza et al. (2014)	Guppies (*Poecilia reticulata*)	Pool-of-competence
Wang et al. (2015)	Zebrafish (*Danio rerio*)	Pool-of-competence

3. Alternative mechanisms for improved cognitive performance in fish shoals

3.1. Individual-level improvements in cognitive performance in groups

Although numerous studies have demonstrated improved performance in larger fish shoals, there is evidence from studies of fish and other animals that other mechanisms can provide (albeit non-mutually exclusive) alternatives to swarm intelligence (Table 1). Firstly, a major driver for the evolution of group living is a reduction in predation risk (Krause and Ruxton, 2002; Ward and Webster, 2016). This can occur because of attack abatement (risk is diluted between individuals when predators can only consume a limited number of prey and the rate of attack is less than proportional to group size, e.g. Santos et al., 2016), the confusion of predators when multiple prey are within the visual field (Ioannou et al., 2009; Lemasson et al., 2016), and collective vigilance for predators (Elgar, 1989; Godin et al., 1988). These effects have been shown to reduce the perception of risk in groups (e.g. Magurran and Pitcher, 1983), allowing individuals to be less vigilant for predators and spend more of their cognitive resources on other activities such as foraging (Goldenberg et al., 2014; Griffin and Guez, 2015; Morgan, 1988). Thus, individuals themselves can afford to devote more of their limited cognitive resources (Dukas, 2002) to other tasks and may show greater cognitive performance in groups, without any information exchange taking place between individuals. If the cognitive task is related to foraging, this effect can also occur as a result of perceived competition for food, which generally increases in larger groups (Grand and Dill, 1999; Johnsson, 2003). This individual-level explanation for improved performance in groups has tended to be the mechanism favoured in older studies showing improved cognitive ability in fish shoals. For example, Smith and Warburton (1992) found blue-green chromis (*Chromis viridis*) in larger groups fed more quickly on concentrated swarms of prey, which they argued was due to a reduced confusion effect as the fish could reduce their anti-predatory vigilance in larger groups. This was supported by further behavioural observations: as the fish fed, feeding became less efficient and shoal cohesion increased, suggesting an increase in perceived risk relative to the need to feed as the fish became satiated.

An interlinked potential problem in experiments is whether the preferences of individuals change as group size increases, which results in changes to motivation at the individual level rather than information being the key factor. Sumpter et al. (2008), using three-spined sticklebacks (*Gasterosteus aculeatus*), attributed the improved ability of groups to discriminate between which of two different replica fish to follow to a quorum decision making mechanism, a well documented way in which bees and ants achieve swarm intelligence (Sumpter and Pratt, 2009). However, this assumes that individuals alone or in small groups are as discriminatory regarding group members' phenotypes as those in larger groups. In moderately sized shoals, the presence of a phenotypically odd individual can increase predation on both the odd and non-odd group members (the "oddity" effect; Landeau and Terborgh, 1986). This suggests that members of larger groups should be more discerning of the phenotypic traits of who they shoal with, while single or pairs of fish may benefit more from following any individual (and hence increasing their group size) compared to the cost of shoaling with a phenotypically different individual. Conversely, if smaller groups are expected to be more discerning, then this would be expected to dampen the apparent improvement of cognitive ability in larger groups. In two studies discussed in more detail below, single fish rather than pairs would be expected to prefer the larger of two groups (Bisazza et al., 2014), and individuals in smaller groups would be likely to be more risk averse, and be more likely to avoid a model predator (Ward et al., 2011). In fact, there is also recent evidence from ants that individuals in smaller colonies compensate for their smaller numbers by working harder, an effect which should decrease the effect of group size on cognitive ability (Cronin and Stumpe, 2014).

3.2. Group diversity: the 'pool-of-competence'

Inter-individual variation has been shown to be important in collective animal behaviour, from variation in overt traits such as sex, body size and age, to less conspicuous variation in traits such as hunger (Nakayama et al., 2012) and risk-taking tendency (Ioannou and Dall, 2016). These traits will often contribute to variation between individuals in knowledge (McComb et al., 2001), motivation (McDonald et al., 2016) and cognitive ability (Trompf and Brown, 2014). Social interactions themselves can even establish or magnify differences between individuals (Bergmüller and Taborsky, 2010; Rands et al., 2003). More knowledgeable, motivated or cognitively able individuals are more likely to influence other group members, and are less likely to be influenced by them (Calovi et al., 2015; Couzin et al., 2005). The greater the variation between individuals in these traits, the more likely group decisions are made by a minority and are followed by the rest of the group (Griffin and Guez, 2015). Larger groups are statistically more likely to contain knowledgeable, motivated and able individuals, which can thus explain improved cognitive performance in larger groups. This is known as the 'pool-of-competence' effect (Morand-Ferron and Quinn, 2011) and is a leading explanation for why rates of problem-solving improve with group size in flocks of birds (Liker and Bókony, 2009; Morand-Ferron and Quinn, 2011). It is also a form of leadership (King, 2010), which is taxonomically widespread including in fish, and has been shown to correlate with holding pertinent information (Ioannou et al., 2015; Reebs, 2000) and motivation (Harcourt et al., 2009). This effect may explain why Godin and Morgan (1985), using banded killifish (*Fundulus diaphanus*), found a strong negative relationship between group size and the variability in the distance groups responded to a model predator. Larger groups are more likely to contain a representative sample of the population and hence be less variable than smaller groups, which is a sample size effect.

4. Distinguishing the mechanisms driving improved cognitive performance in groups

4.1. Fish studies

A handful of recent empirical studies have gone some way toward distinguishing the mechanisms that result in greater cognitive performance in groups, highlighting the different approaches, and also the difficulty in doing so. Ward et al. (2011) demonstrated that larger shoals of mosquitofish (*Gambusia holbrooki*) were faster and more accurate in avoiding a model predator in one arm of a Y maze. In a later study, Bottinelli et al. (2013) developed an individual-based model of fish shoaling in the Y maze that recreated both the improved accuracy of larger groups and the movement characteristics of the fish during decision making. That a model with individual behaviours representative of collective motion in real fish could explain these experimental results is good support for a swarm intelligence mechanism. As the decision making context was one of predator avoidance, it is also less likely that the improved performance could alternatively be explained by individuals having a reduced perception of risk as in this case avoidance of the predator would be reduced in larger groups. It is conceivable that grouping reduces risk more for particular types of predator (Cresswell and Quinn, 2010; Neill and Cullen, 1974), allowing fish to be less vigilant (for example) for aerial predators and more vigilant for sit-and-wait predators such as simulated by the model predator in the Ward et al. study. This has yet to be tested, however.

Ward et al.'s study is also a rare case using fish where it was tested whether the improved decision making in larger shoals was because these were more likely to contain better performing individuals. Fish were tested alone repeatedly 9 times to determine whether some individuals had a better ability to avoid the model predator. The observed distribution of the number of times individuals avoided the predator did not differ compared to that expected from a random distribution, suggesting that there was no consistent differences between individuals. However, the reliance on a non-statistically significant result raises an issue that is relevant to experimental studies of group decision making more generally: it is relatively straightforward to show that group decisions are disproportionately influenced by particular individuals, for example the boldest (a positive result, $P < 0.05$), but much more difficult to demonstrate that a negative result ($P > 0.05$) is due to egalitarian group decision making rather than a lack of statistical test power. In the case of Ward et al.'s study, a larger sample of fish may have pushed the P value below 0.05 and altered the conclusions drawn in the study. This is a major drawback to using P values in statistical inference.

Independently of this statistical issue, it is also not clear whether the cognitive performance of an individual when tested alone is representative of its performance in a group, which is related to the point above regarding reduced perception of risk by individuals in groups. Isolating individuals from groups in animals that have evolved to be social, including many species of fish, can cause stress (Hennessy et al., 2009; Reid and Latty, 2016), as evidenced by changes in stress hormones (Galhardo and Oliveira, 2014) and metabolic rate (Nadler et al., 2016). Relative differences between individuals may change when tested alone or in a social context, as well as average levels of performance. A more useful approach and potential challenge for future studies is to quantify the relative contributions of individual differences and swarm intelligence to collective performance. This is particularly important as it is likely that different mechanisms operate simultaneously in real animal groups (Morand-Ferron and Quinn, 2011). This would involve quantifying individual performance of group members but in a way that is representative when individuals interact freely in groups, and ideally manipulating group membership and group size in a controlled way to determine the relative contributions of each effect. A classic study by Pitcher et al. (1982) went some way toward this kind of design. They showed that larger shoals found a hidden food source more quickly, and also demonstrated there was no average difference between focal individuals in their foraging performance when they were tested across trials in different shoal sizes (note that "solitary fish were not included as controls because pilot work indicated they behaved aberrantly": Pitcher et al., 1982). Although evidence against the pool-of-competence in foraging fish shoals, in principle this mechanism does not necessarily rely on variation between individuals being consistent. Instead, there may be population-level variation in performance but this changes between individuals over time, for example due to hunger altering motivation. Such an effect would be much more difficult to tie down and quantify experimentally compared to consistent individual variation in performance that can be quantified through repeated testing of known individuals.

Another recent study that has shed light on how swarm intelligence can occur in fish shoals used a different experimental approach. Berdahl et al. (2013) gave 1–256 golden shiners a gradient tracking task by projecting moving patches of dark areas onto the bottom of a large test arena, where darkness is preferred by these fish. Here we found that larger groups were better able to track the darker patches, measured as the darkness level at the positions of the fish averaged over time and fish, with a significant improvement in performance even between the largest group sizes (128 versus 256 fish). At these group sizes, we would expect that individual fish would not change their perception of competition or risk, either because they cannot perceive being in a large group or a larger group twice the size, or because there is little effect of group size on competition or predation risk at this scale and hence no reason to modify behaviour (Rieucau et al., 2014). Although the pool-of-competence effect could not be ruled out, our study did link observed behaviours of individuals to the mechanism underlying the improved cognitive performance, which met the requirements of swarm intelligence. From trajectories of individual fish, Berdahl et al. observed that fish did not accelerate toward darker areas, but instead they moved toward areas more densely packed with shoalmates. As darker areas tended to have more fish as individuals responded to the level of darkness in their local vicinity by slowing down (which also decreased inter-individual spacing), these darker areas became more attractive because of the other fish being more likely to occupy these areas. These behaviours were then incorporated into an individual based model of shoaling and there was a good match between model derived and experimental results, supporting the proposed mechanism for how swarm intelligence arose in these experiments via local interactions and self-organisation.

However, it is yet to be shown whether the mechanism found to underlie this swarm intelligence generalises more widely. One feature of our design was to use shallow water of 8 cm, which is realistic for these fish (Hall et al., 1979) and often used in studies of collective behaviour to facilitate computer tracking. However, this would have limited individuals' abilities to see the level of darkness further away. Thus the fish's use of social information (moving toward areas with other fish) compared to personal information (moving directly toward dark patches) may be greater than that usually observed. In other words, individual level cognitive ability to move to dark areas may have been limited by the experimental design. More experiments are needed to test whether varying water depth would change the group size effect on performance and the weighting of personal and social information, although this may introduce further confounding effects as perception of risk may change in deeper water (e.g. Harcourt et al., 2009).

In contrast to this use of large group sizes (at least relative to laboratory studies), Bisazza et al. (2014) compared numerical acuity (the ability to distinguish between numbers) between single

fish and pairs of guppies (*Poecilia reticulata*). In both an ecologically relevant task of distinguishing between two shoals of different sizes and an abstract task of distinguishing between two stimuli with a different number of black dots (while controlling for stimulus surface area, etc.), pairs of fish outperformed individuals tested alone. Moreover, the average performance of the pairs was compared to simulated pairs made up of randomly selected individuals tested alone. Average performance of the real pairs matched closely the best performing individual in the simulated pairs, and outperformed the average performance of the two individuals in the simulated pairs. This provides convincing evidence for a pool-of-competence effect, where the better individual led the group decision in the trials with two fish. A similar effect was also found by Wang et al. (2015), where the speed and accuracy of pairs of zebrafish in a colour discrimination task was not significantly different to the individual that tended to make slower but more accurate decisions when tested alone.

4.2. Other vertebrates

To distinguish the 'pool-of-competence' from improved individual level performance in larger groups, two recent studies of bird flocks have used different approaches. Liker and Bókony (2009) demonstrated that larger groups of house sparrows (*Passer domesticus*) were faster to innovate in a novel foraging task and opened more of these feeders. By examining the effect of group size on other behaviours, they argued that there was no evidence that individual-level performance would be better in larger groups, for example due to reduced anti-predatory vigilance. This involved showing no effect of group size on the proportion of individuals attempting to solve the task, the rate of attempts per individual, latencies to first approach the task or individual scan rates. In a separate neophobia test, there was no difference between small and large groups in the latency to approach a novel object. The study concluded that the most likely explanation for better performance in groups was the pool-of-competence effect, although they did not show direct evidence for this mechanism. Again, a reliance on non-significant statistical tests to rule out competing hypotheses is not without problems, as discussed above.

In a later study, Morand-Ferron and Quinn (2011) used naturally occurring flocks of great (*Parus major*) and blue (*Cyanistes caeruleus*) tits, again studying their ability to innovate in opening novel feeding devices. The authors used multiple lines of evidence to determine whether the pool-of-competence or a reduced perception of risk could explain the observed improvement in problem solving with group size (measured as a greater proportion of feeders opened). As in the study by Liker and Bókony (2009), latency to approach the feeders was not related to group size, suggesting birds were not more neophobic in smaller groups. Feeders were also placed near and far from vegetation to manipulate perceived predation risk, and although the proportion of feeders opened was greater closer to cover, the relationship between group size and performance was not more steep further from cover, suggesting a reduction in risk in larger groups was not driving the group size effect (see Grand and Dill, 1999). The strongest and most direct evidence for the pool-of-competence came from being able to individually identify birds, as flocks containing at least one individual previously observed to have solved the task increased group performance. Examining only individuals that solved the task at least once, the authors also demonstrated consistent individual variation in the probability to solve the task per visit, but also an improved ability per individual with the number of companions present, supporting a reduced perception of risk in larger groups contributing to solving ability. Thus, there was evidence for both mechanisms to be operating in this system.

The mechanism for better performance in larger groups was also inferred by the shape of the relationship between group size and performance on the task. The pool-of-competence mechanism was argued to be supported based on the linear relationship observed between group size and performance, while if driven by a relaxation of cognitive resources from anti-predatory vigilance, there would be a saturating effect as group size increased (as observed in studies of vigilance in bird flocks, e.g. Fernandez-Juricic et al., 2007). However, theoretical work has argued that these two mechanisms cannot be distinguished based only on the shape of the observed relationship between performance and group size (Griffin and Guez, 2015). The relationship between group size and performance, if caused by a pool-of-competence effect, is likely to be determined by the type of problem individuals are trying to solve and the extent to which information is transferred between individuals. If a certain proportion of the group needs to be informed, motivated and/or able, larger groups will not show an increased level of performance from the pool-of-competence. If instead a particular number of individuals is required (e.g. Couzin et al., 2005), then on average, group performance should increase with group size, as larger groups are more likely to contain the required number of individuals. How and to what extent information is transferred through the group from those that directly respond to a stimulus will be a major determining factor (Attanasi et al., 2014; Handegard et al., 2012; Herbert-Read et al., 2015). In all cases, from a purely statistical process, there will be less variability between larger groups compared to between smaller groups (as found in the study of vigilance by Godin and Morgan, 1985, discussed above).

5. Ecological and evolutionary factors

A major difference between shoals of fish (and most other collectives of vertebrates) and a colony of social insects is the degree of relatedness between individuals. Recognition and preferential shoaling with kin and familiar individuals is well documented in fish (Frommen et al., 2007; Kamel and Grosberg, 2013; Ward et al., 2007), and some species form stable, small groups of related individuals (most notably numerous species of cichlid and reef fish: Bshary et al., 2002). Cooperating with kin provides inclusive fitness benefits, and repeated interactions with the same individual favours reciprocal altruism (Fletcher and Zwick, 2006; Hesse et al., 2015), both of which would favour overall group cognitive performance rather than behaviours to exploit others in the group. Most gregarious species of fish however show fission-fusion dynamics where individuals frequently exchange membership of groups (Ioannou et al., 2011), so that groups are primarily made of unrelated, unfamiliar individuals which increases conflicts of interest and favours selfish rather than cooperative behaviour. Thus, behaviours that drive group intelligence at the level of the individual must provide short term benefits as well as resulting in improved averaged cognitive performance over the group. This is in stark contrast to social insect colonies, where collective cognition often occurs within sterile worker castes that rely on the colony's reproductive success for their inclusive fitness (Couzin, 2009; Seeley, 2010, 2009), to the point where the colony can be considered a "super-organism" (Wilson and Hölldobler, 2009). Thus, we should expect selection pressure on group intelligence to be much stronger in social insects compared to fish shoals, and hence be more developed and sophisticated.

Relatedness within groups and membership stability could explain why there are clearly specialised behaviours that have evolved in social insects that facilitate collective decision making, for example tandem running in ants (Shaffer et al., 2013) and the waggle dance in bees (Biesmeijer and Seeley, 2005). Similarly, intentional vocal signals are used to transfer information within

groups of mammals (Bousquet et al., 2011; Seyfarth et al., 1980) and birds (Bell et al., 2009), although these groups also differ from typical shoals of fish as they tend to be made up of related individuals and have stable membership over time. There is little evidence currently of equivalent active communication in fish, where instead the mechanisms for information transfer that drive group decisions are believed to be the same as those for group formation and maintenance, i.e. based on positions and movements of near neighbours in a group. In other words, no obvious signals seem to have evolved specifically for information transfer during group decision making. This is in contrast to the use of signals by fish to transfer information in non-group decision making contexts such as reproduction (Slabbekoorn et al., 2012), aggression (O'Connor et al., 1999) and cooperation (Grutter, 2004). It is surprising that acoustic signals in particular do not seem to be used by shoaling fish during group decisions since the reduced visibility in water compared to air (especially under turbid conditions) and greater transmission of sound in water would make this an ideal modality with which to actively transfer information (Ladich, 2000). Of course, the lack of signals may reflect the high efficiency of changes in motion to transfer information within shoals, or there may be ecological constraints such as eavesdropping by predators (Magnhagen, 1991). Exploring the evolution of active signals across taxa under different ecological and social conditions should shed light on why such signals have evolved in some systems and not others.

Another interesting area for future research is to relate individual and collective levels of cognitive ability (Couzin, 2009). Fish can show a wide range of advanced cognitive abilities, and there are more aspects of social behaviour in fish than just the optimisation of collective decision making (Brown et al., 2006; Bshary et al., 2002). On the one hand, social behaviours such as reciprocal cooperation, deception and forming coalitions select for increased cognitive ability in individuals (the social brain hypothesis: Dunbar, 1998). All else being equal, average group size of a species would positively correlate with cognitive ability of individuals. On the other hand, a high degree of group-level performance may relax selection on individual level cognitive ability (which is costly) and would then correlate negatively with average group size. A recent comparative analysis of wasps suggests that investment in brain structures does in fact decrease in social compared to solitary species, supporting a "distributed cognition hypothesis" rather than the social brain (O'Donnell et al., 2015). Comparative studies of fish are fairly common (Seehausen et al., 1999; Tsuboi et al., 2014) and it would be fascinating to see whether the complexity of social behaviours (e.g. deception) and reliance on group intelligence could explain differences in the relationship between average group size and individual cognitive ability.

It is also worth giving some consideration to whether there are ecological or evolutionary consequences of improved cognition in groups being based on different mechanisms. Although little research has addressed this question, it is clear from other research on complex systems that disproportional influence of particular units in a network, whether they be a keystone species in an ecosystem (Solé and Montoya, 2001), 'super-spreaders' in a disease network (Adelman et al., 2015; Wong et al., 2016) or knowledgeable individuals in a group (McComb et al., 2001), makes the network structure susceptible as loss of influential units has a large effect on the network as a whole. Thus, group decisions based on the distributed swarm intelligence (Fig. 1d) may be particularly robust to the loss of individuals from the group due to disease or predation as they do not rely on particular individuals acting as leaders or as hubs for the aggregation of information. In a similar manner, distributed swarm intelligence in animals may be more robust to some individuals influencing the outcome of the decision to favour their own self-interest, which may be especially true in many fish species where groups are made up largely of unrelated individuals that do not form stable bonds, as discussed above.

A potential disadvantage, however, to swarm intelligence compared to decisions being made by a minority of individuals is its speed. Although not demonstrated explicitly, it would be expected that the repeated interactions between individuals that take place during distributed group decision making is slower than a more linear spread of information from a single individual acting as a leader. Decisions where speed is a critical factor, for example whether individuals should respond to a potential predator, may show a simpler network of inter-individual interactions to minimise the number of connections and maximise response speed (Fig. 1c). Indirect evidence for this comes from ants, where the quorum threshold required for a colony to make a decision decreases in harsh conditions (Cronin, 2016; Franks et al., 2003), which speeds up decision making and shifts it from more of a collective to an individual-level decision (Franks et al., 2003). It should also be recognised that simply having distributed, self-organised interactions in groups does not always result in swarm intelligence when facing cognitive tasks. The network of interaction between individuals requires calibration (Kennedy et al., 2001), which in animal groups has occurred through a process of natural selection over many generations and resulted in relatively cognitively simple individuals being able to solve difficult problems when acting collectively (Berdahl et al., 2013; Reid et al., 2016; Sasaki et al., 2013). However, experimental manipulations show swarm intelligence in animal groups can be limited, for example with groups of ants or caterpillars failing to exploit better food sources as a result of an established foraging trail to an inferior food source (Beckers et al., 1993; Dussutour et al., 2007). This suggests that such systems may be relatively inflexible in evolutionary novel contexts, with potential innovation by individuals being suppressed.

6. Conclusion and recommendations for future work

The examples discussed above demonstrate the diversity of contexts in which group decision making occurs. As with decision making in individuals, decisions can be single events (e.g. finding a food source (Pitcher et al., 1982) or avoiding a predator (Ward et al., 2011)) or continuous, being made of many sequential decisions, such as tracking an odour gradient (Grünbaum, 1998). Some tasks are suitable for a single individual to perform, which is then copied by neighbours and spreads through the group (Godin and Morgan, 1985; Liker and Bókony, 2009), while others rely on the spatial spread of individuals in the group to improve average cognitive performance (Berdahl et al., 2013; Pita et al., 2015). This diversity is likely to be reflected in variation in the mechanisms driving group-level intelligence; different requirements of the task and the extent of variation between individuals in relevant traits such as motivation or ability will favour different mechanisms. It is also worth reiterating that the different mechanisms discussed here are not mutually exclusive, and in real world animal groups it is probably common for a combination of mechanisms to be operating simultaneously to generate improved performance in groups (Morand-Ferron and Quinn, 2011). This is in contrast to the tendency of most studies to favour a particular mechanism to explain their observed results (Table 1). The issues discussed in this review highlight the difficultly in experimentally demonstrating self-organised swarm intelligence in animals, and will hopefully help researchers design new experiments that can shed light on this phenomenon (Table 2).

In contrast to many topics in animal behaviour, including other aspects of social behaviour (Elgar, 2015), studies of collective behaviour often seek the commonalities in trends and underlying mechanisms that apply across seemingly disparate systems,

Table 2
Summary of potential experimental approaches to help distinguish swarm intelligence from other mechanisms that also lead to improved cognitive performance in groups. The example references do not themselves necessarily show improved performance in larger groups, nor are they exclusive to studies on fish.

Method	Example reference(s)
Describe mechanism(s) for how local interactions scale to the group decision and improved performance	Berdahl et al. (2013)
Map network of local interactions within the group during group decision making	Strandburg-Peshkin et al. (2013)
Quantify extent of variation between individuals in task performance when tested alone	Wang et al. (2015), Ward et al. (2011)
Track performance of all/focal individuals repeatedly tested in groups	Bisazza et al. (2014), Morand-Ferron and Quinn (2011), Pitcher et al. (1982)
Measure other behaviours that indicate a non-swarm intelligence mechanism, e.g. reduced vigilance in larger groups	Liker and Bókony (2009), Magurran and Pitcher (1983)
Manipulate motivation (hunger, predation risk) as well as group size to separate individual-level from group-level effects	Grand and Dill (1999), Morand-Ferron and Quinn (2011), Morgan (1988)
Test whether the variance in performance between groups at a particular group size is affected by group size	Godin and Morgan (1985)
Demonstrate improved cognitive performance over group sizes too large for individual fish to be able to perceive these differences in shoal size	Berdahl et al. (2013)
Quantify the shape of the relationship between group size and performance	Morand-Ferron and Quinn (2011)

whether these be an ant colony or a fish shoal (e.g. Arganda et al., 2012), and even extending to systems beyond groups of non-human animals such as pedestrian crowds (Moussaid et al., 2009) and neural systems (Couzin, 2009; Passino et al., 2008). This often involves assuming individuals follow relatively simple behavioural rules that are still adequate to explain the observed collective behaviour. While a major strength of this field as it allows broadly applicable principles to be identified (Sumpter, 2006), other aspects of an animal's behaviour may throw a spanner in the works when models are being tested against empirical data (Gordon, 2007). This is particularly true when the complexity of individuals is oversimplified. There is little doubt that swarm intelligence occurs in social insects such as bees and ants, and there is a large body of experimental and theoretical evidence demonstrating the detailed mechanisms for how swarm intelligence occurs (e.g. Biesmeijer and Seeley, 2005; Bonabeau et al., 1999; Campo et al., 2011; Shaffer et al., 2013). In the case of swarm intelligence in fish shoals, there is substantial experimental evidence for alternative mechanisms for better performance in groups, namely individual-level cognitive effects of being in a group and variation between individuals that can result in some leading others (Table 1). Thus, even when experimental data fit a model of behaviour based on a swarm intelligence mechanism, other, very different, mechanisms may provide equally good fits (Sumpter et al., 2012). It is important to note that the success of demonstrating swarm intelligence in social insects has come from documenting the behaviours and processes that underlie group decision making, rather than ruling out other ways in which improved performance in groups can arise. In contrast, the behavioural observations for how swarm intelligence could occur in other groups of animals are rarely demonstrated (but see Berdahl et al., 2013).

Fish have been a popular taxonomic group with which to study social behaviour. Many species are small enough to keep sufficiently large numbers of individuals and groups under laboratory conditions. This allows for the testing of large group sizes, and the testing of an adequate number of independent groups to be able to make inferences about the source population as a whole (a point recently made by Vogel et al. (2015) regarding slime moulds). Moreover, due to the fission-fusion social structure of many of these species, they are naturally found at a range of group sizes (Ioannou et al., 2011), and group membership can be manipulated easily with minimal stress or aggression. Thus they allow the rigour and control of testing in the laboratory like ants (e.g. Collignon and Detrain, 2014; Shaffer et al., 2013), while showing similar inter-individual communication and patterns of movement to those of birds where studies of collective behaviour are often limited to field studies (Attanasi et al., 2014; Pettit et al., 2015). For these reasons and the ability to track individuals in groups, fish hold great potential to contribute to understanding the mechanisms that can result in group intelligence. However, like most groups of animals, information is not the only reason they form and maintain groups (experimentally shown by Miller et al., 2013), and individuals are more cognitively complex than models assume (Bshary et al., 2002). Although assuming simplicity of individual agents when modelling collective behaviour allows models to be generic and tractable, researchers should strive for the broadest possible understanding of cognition and behaviour to recognise the limitations of these simplifying assumptions. The challenge for empiricists is to design experiments and analyses that consider these effects and quantify the contribution of swarm intelligence to improved cognitive performance in groups relative to other potential mechanisms, and to identify the behaviour(s) at the level of the individual that result in swarm intelligence.

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