

Oddity, predation risk and social decisions in aquatic invertebrates

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Abstract

Group living is widespread across animal taxa, incurring benefits such as increased foraging efficiency or an enhanced chance of surviving a predator's attack. The chances of escaping a predator are often lower for odd-looking individuals, as these are detected at a higher rate than uniform looking group members. While this "oddity effect" shall operate in animals differing in any given phenotype, including colour, size or species identity, it has been experimentally tested mainly for odd-coloured individuals. We examined the oddity effect and swarming preferences in two differently sized species of freshwater planktonic crustaceans (large *Daphnia magna* and small *Daphnia pulex*). We experimentally investigated whether odd individuals in a swarm of heterospecific *Daphnia* were more vulnerable to predation by a common predator, the three-spined stickleback (*Gasterosteus aculeatus*). Furthermore, *Daphnia's* swarming preference was tested by giving individuals the opportunity to choose between conspecific/heterospecific odour and a neutral control. In contrast to the predictions of the oddity effect, odd individuals were not always preyed on earlier; instead three-spined stickleback preferentially predated large, more nutritious individuals. *Daphnia* of both species reacted towards the perception of con- and heterospecifics odours. While *D. pulex* generally avoided the smell of other daphnids, *D. magna* avoided conspecifics but tended to prefer heterospecifics over the neutral control. These findings provide new insights into swarming strategies and social preference of an invertebrate and how this behaviour can influence predation risk.

KEYWORDS

confusion effect, *Daphnia*, selfish herd, shoaling, social preference, three-spined stickleback

1 | INTRODUCTION

Group living is widespread across animal taxa, incurring several benefits for individuals, such as increased foraging efficiency (Pitcher, Magurran, & Winfield, 1982; Tanaka, Frommen, & Kohda, 2018), higher chances to find a high-quality mating partner (Roff, Doropoulos, Mereb, & Mumby, 2017; Wedekind, 1996) or energy savings (Marras et al., 2015; Trenchard & Perc, 2016). Still, the most studied cause of group living and aggregation is the reduction of

predation risk (Groenewoud et al., 2016; Herbert-Read et al., 2017; Krause & Ruxton, 2002; Turner & Pitcher, 1986), although for some taxonomic groups other benefits are assumed to play a superior role (Rieucau, Fernö, Ioannou, & Handegard, 2015). There are several mutually non-exclusive explanations of how group living enhances an individual's chance of surviving a predator's attack, such as risk dilution (Foster & Treherne, 1981), selfish herd effects (Hamilton, 1971) or predator confusion (Krakauer, 1995; Miller, 1922). In the latter, attack success of predators is lowered due to a sensory overload

and the inability to accurately select an individual prey within a moving group (Krakauer, 1995; Tosh, Jackson, & Ruxton, 2006).

A predator strategy to counteract the confusion effect is to focus on more conspicuous, phenotypically odd-looking prey in an otherwise homogenous group. This "oddity effect," where individuals that differ in body size (Rodgers, Downing, & Morrell, 2015; Theodorakis, 1989), colour (Landeau & Terborgh, 1986; Ohguchi, 1978; Pielowski, 1959) or species (Almany, Peacock, Syms, McCormick, & Jones, 2007) are targeted more readily, has been investigated in mammals, birds, fishes and invertebrates alike. For example, American kestrels (*Falco sparverius*) preferentially target on odd-coloured mice (*Mus musculus*) (Mueller, 1975), goshawks (*Accipiter gentilis*) selectively prey on rare colour variants of feral pigeons (*Columba livia*) (Rutz, 2012) and largemouth bass (*Micropterus salmoides*) favourably attack odd-sized individuals in three different minnow species (*Pimephales notatus*, *P. promelas* and *Camptostoma anomalum*) (Theodorakis, 1989). Still, predators readily include other factors in their foraging decisions, such as the fullness of their own stomach (Gill & Hart, 1994) or the nutritional value of the prey (Nuutinen & Ranta, 1986). Here, larger prey items are expected to be of higher nutritional value but might at the same time be more difficult to handle (e.g., Nilsson, Brönmark, & Pettersson, 1995). However, such trade-offs will vanish in cases where the size difference between the predator and prey is large, like in many fishes targeting on small invertebrates (e.g., Gill & Hart, 1994).

To minimise oddity effects, prey animals are expected to choose phenotypically similar groups, as in such case visual hunting predators are less precise in their attacks, resulting in a lower individual risk of predation (Jeschke & Tollrian, 2007; Krakauer, 1995; Milinski, 1984). Accordingly, homogenous aggregations are widespread across fishes (Krause, Godin, & Brown, 1996; Ward, Axford, & Krause, 2002), mammals (Meldrum & Ruckstuhl, 2009) and birds (Smith, King, & West, 2002; Sridhar et al., 2012). However, animals base their social decision not only on phenotypic uniformity. Indeed, there exist a pleiotropy of features that are of importance, including nutritional state (Frommen, Luz, & Bakker, 2007; Morrell, Hunt, Croft, & Krause, 2007), competitive abilities (Metcalf & Thomson, 1995), group size (Hoare, Couzin, Godin, & Krause, 2004; Thünken, Eigster, & Frommen, 2014), familiarity (Frommen et al., 2007; Griffiths & Magurran, 1998), relatedness (Arnold, 2000; Frommen et al., 2013) or species identity (Ward et al., 2002). Furthermore, several of these factors might be integrated, leading to groups that show considerable phenotypic variation (e.g., Farine, Garroway, & Sheldon, 2012; Fitzgibbon, 1990; Goodale, Beauchamp, & Ruxton, 2017; Hoare, Krause, Peuhkuri, & Godin, 2000). This indicates that other benefits of group membership might outweigh the costs of being conspicuous within the group. During social decisions, prey individuals should therefore trade-off risks of oddity and conspicuousness against other costs and benefits associated with group formation (Krause & Ruxton, 2002; Rodgers, Kimbell, & Morrell, 2013).

Thus far, most studies exploring oddity effects focused on monospecific prey, manipulating its colouration or density (Milinski, 1977; Ohguchi, 1978). However, it remains unclear how generalisable such

effects are. For example, in aggregations of different-sized individuals, larger individuals might not only be more conspicuous and easier to target than smaller ones but are further expected to be at greater risk of predation due to their higher nutritional value (Gill & Hart, 1994). Indeed, many predators preferably target on large prey (e.g., Li, Wetterer, & Hairston, 1985; Wetterer & Bishop, 1985). For example, Rodgers et al. (2015) found that larger *Daphnia magna* are at greater risk of being attacked by three-spined stickleback (*Gasterosteus aculeatus*) compared to smaller ones, independent of oddity effects. Still, in a group of large individuals a small one would be perceived as odd, making it easier for a predator to overcome the confusion effect and therefore being targeted first. Thus, predictions derived from optimality theory (Manatunge & Asaeda, 1998; Mittelbach, 1981), postulating that a predator should target the prey of higher nutritional value, are sometimes in contrast to the oddity effect. Thus far, our knowledge of how the risk of being the odd one out in a multispecies group differing in size and how this risk influences social decisions is scarce. This shortcoming is unfortunate, as it hampers our understanding of the drivers shaping multispecies animal aggregations.

Grouping behaviour as an anti-predator response has been well studied in vertebrates (Almany et al., 2007; Ioannou, Bartumeus, Krause, & Ruxton, 2011; Jones, Croft, Ramnarine, & Godin, 2010; Milinski, 1977; Morse, 1977; Tosh et al., 2006). However, much less is known on the anti-predator benefits of aggregation behaviour in invertebrates (Durieux, Rigaud, & Medoc, 2012; Kullmann, Thünken, Baldauf, Bakker, & Frommen, 2008; Lima & Dill, 1990; Ritz, 1994; Roozen & Lüring, 2001; Thünken et al., 2010; Vulinec, 1990). Daphnids are freshwater planktonic crustaceans (McCauley & Murdoch, 1987; McCauley, Murdoch, Nisbet, & Gurney, 1990), with several species regularly co-occurring in the same habitat (Hanski & Ranta, 1983; Pajunen & Pajunen, 2003). They represent an important food source for many fish species (Brooks & Dodson, 1965), with odd-coloured individuals facing a higher risk of predation (Ohguchi, 1978; Penry-Williams, Ioannou, & Taylor, 2018; Rodgers et al., 2013). Daphnids are well known for their impressive phenotypic plasticity and morphological responses to changes in predation risk (Beckerman, Rodgers, & Dennis, 2010; Laforsch & Tollrian, 2004; Tollrian, 1995). They further show various behavioural responses to the risk of predation, such as horizontal and vertical migration and reduced activity (Tollrian & Dodson, 1999). Furthermore, they form aggregations (Folt & Burns, 1999; Irvine, 1989; Tollrian & Dodson, 1999), especially in high-risk populations. Their main sources of information about their social and predatory environment are olfactory cues, which they use to detect the presence of predators and competitors (KleivenLarsson & Hobæk, 1996; Larsson & Dodson, 1993; Pijanowska, 1994; Roozen & Lüring, 2001). These features make daphnids an ideal model organism to study the oddity effect in groups composed of individuals of different species that differ in nutritional value, and to further elucidate how this variation in predation risk is reflected during social decisions in these species.

In the present study, we examined the oddity effect in differently sized prey, using *D. pulex* and *D. magna* as study species, and

three-spined stickleback as predator. Further, we explored how social preferences in aquatic invertebrates affect the formation of mixed-species groups. In a first experiment, we allowed three-spined stickleback to predate on mixed *Daphnia* aggregations, either containing several large *D. magna* and a single small *D. pulex* or vice versa. In case of oddity effects taking place, we predict that odd individuals are targeted earlier than expected by chance. In contrast, if three-spined stickleback's predatory behaviour is mainly driven by optimal energy intake, we predict that large *D. magna* generally face higher risk of predation. In a second experiment, we tested olfaction-based aggregation preferences in both *Daphnia* species, providing the choice between a conspecific or heterospecific stimulus and a blank control. We predicted that both *Daphnia* species include species identity in their grouping decisions in order to maximise predator protection.

2 | MATERIALS AND METHODS

2.1 | Experimental subjects

Three-spined stickleback were used as predators, which are well known to prey on *Daphnia* (Modarressie & Bakker, 2007; Rodgers et al., 2013). Adult three-spined stickleback were caught from a large, genetically heterogeneous population on the island of Texel, the Netherlands (Heckel et al., 2002), in spring 2006. Fish were kept in an outdoor tank (720 L) and were fed in excess on *Chironomus* larvae once a day. The size of the fish used in the experiments was 5.2 ± 0.11 cm (mean \pm SE, range: 4.2–6.4 cm), and the body condition (weight [g] \times 100/standard length [cm]³) (Bolger & Connolly, 1989) was 1.21 ± 0.05 g/cm³ (mean \pm SE, range 0.95–1.52 g/cm³). Experiments took place before the daily feeding of the fish; therefore, all focal three-spined stickleback were food deprived for at least 18 hr.

Daphnia pulex and *D. magna* were used as prey in the experiments. These species differ remarkably in body size (Hanski & Ranta, 1983) and often co-occur in the same habitat in the wild (Pajunen & Pajunen, 2003). They were collected from predator-free outdoor mesocosms at the University of Bonn and from predator-free ponds in northern Finland. *Daphnia* from Bonn and Finland were never mixed to avoid population-based effects. In the laboratory, all *Daphnia* were fed the same mix of green algae ad libitum (Ebert, D. Web-guide to *Daphnia* parasites, <http://evolution.unibas.ch/ebert/lab/algae.htm>). All *Daphnia* were kept under summer light conditions, with a 16:8 light:dark cycle and a water temperature of $17 \pm 1^\circ\text{C}$. All *Daphnia* and three-spined stickleback were used only once to avoid pseudoreplication.

2.2 | Predation experiment

The experiments were conducted in a plastic test tank ($40 \times 21 \times 25.5$ cm, l \times w \times h), which was divided into a small ($10.5 \times 21 \times 25.5$ cm) and a large compartment ($29.5 \times 21 \times 25.5$ cm) by a removable, opaque, dark grey plastic divider. The

smaller compartment served as acclimation chamber for the predator, while the larger one served as experimental compartment, in which the respective *Daphnia* groups were presented. As light source, a 36 W fluorescent tube was placed 17 cm above the tank. To prevent disturbance of the fish, white Styrofoam was placed around all sides of the tank. In the front, a small spy hole allowed to observe the experiment. In addition, the inside walls of the tank were covered with dark grey plastic to create a darker environment. Only the front part of the large compartment was not covered, creating a lighter area. As *Daphnia* show strong phototaxis (Dice, 1914), this helped keeping the group more compact. Before the start of each trial, we filled the tank with 1-day-old tap water to a level of 10 cm.

In experiment (1a), swarms of ten small *D. pulex* and one large *D. magna* were used as prey. All *D. pulex* were smaller (as measured from the apex of the head to the base of the spina) than the respective *D. magna* (Wilcoxon matched-pairs signed-rank test: $N = 10$, $Z = -2.805$, $p = 0.005$, *D. magna* (mean \pm SD) 3.89 mm \pm 0.47 mm, mean *D. pulex* 2.12 mm \pm 0.06 mm). The focal three-spined stickleback was introduced into the small compartment behind the divider. Afterwards, the *Daphnia* swarm was placed in a small, transparent plastic cylinder in the centre of the lighter part of the large compartment of the test tank. The cylinder was vertically divided into three equal-sized zones (each of 3 cm height). After 5 min of acclimation, the experiment started. As soon as all *Daphnia* were aggregated in one of the three zones, the opaque divider and the cylinder were removed, allowing the three-spined stickleback to predate the *Daphnia*. The order in which the *Daphnia* were eaten was recorded and the experiments ended when the *D. magna* was eaten by the predator.

In experiment (1b), swarms of ten *D. magna* and one *D. pulex* were used as prey. The respective *D. magna* were larger than the *D. pulex* (Wilcoxon matched-pairs signed-rank test: $N = 15$, $Z = -3.408$, $p = 0.001$, *D. pulex* (mean \pm SD) 1.8 mm \pm 0.14 mm, *D. magna* 2.9 mm \pm 0.28 mm). The procedure was the same as in experiment (1a). Again, the order in which the *Daphnia* were eaten was recorded, the trials ended when the *D. pulex* was eaten by the predator.

2.3 | Social preference experiment

To understand how the aggregation behaviour in these species is affected by species identity, we conducted social preference tests. In experiment (2a), the focal *D. pulex* was allowed to choose either between chemical cues derived from conspecifics (*D. pulex*, $N = 10$) or heterospecifics (*D. magna*, $N = 10$) and a blank tap water "no odour" stimulus. The tests were performed in a tank measuring $17 \times 11 \times 11$ cm, illuminated by a 36 W fluorescent tube placed 32 cm above the tank. On the bottom outside of the tank, three compartments were marked, each measuring 5.7×11 cm. The left and right compartment served as choice compartments, while the middle one served as neutral zone. Above the left and right choice compartments, two plastic tubes (diameter 1.3 mm) were installed, through which stimulus water could be added in

the tank by a peristaltic pump (Ismatec Reglor Digital peristaltic pump ISM 831). Before the start of each trial, we filled the tank with 1-day-old tap water to a level of 3.5 cm. For odour extraction, 30 *D. pulex* or *D. magna* were placed in 11 ml of 1-day-old tap water in a small plastic cylinder that was closed with a plug. After 5 hr, the *Daphnia* were removed using a plastic pipette and the odour water in the cylinders was connected to the tubes of the pump. For the “no odour” stimulus, 11 ml of 1-day-old tap water was used that was treated in the same way. To avoid side biases, the side on which the odour stimulus or the no odour stimulus was pumped into the tank was first randomly assigned by flipping a coin and then altered accordingly between trials. The order of the conspecific and heterospecific odour trials was as well first randomly assigned and then altered accordingly between trials. In experiment (2b), *D. magna* served as focal individuals and were allowed to choose either between chemical cues derived from conspecifics (*D. magna*, $N = 25$) or heterospecifics (*D. pulex*, $N = 19$) and a blank tap water stimulus. All test and stimulus *Daphnia* were used only ones.

At the beginning of each trial, the focal *Daphnia* was placed in a plastic cylinder in the centre of the middle compartment, where it could acclimatise for 5 min. Then, the peristaltic pump was started, pumping 1 ml of stimulus and control water each minute into the respective stimulus compartment. As soon as the odour water reached the test tank, the cylinder was lifted to release the focal *Daphnia*. For a period of 10 min, the position (left, middle, right compartment) of the *Daphnia* was recorded every 30 s (Kullmann et al., 2008; Thünken et al., 2010), resulting into 20 position measurements per individual.

2.4 | Statistical analyses

Analyses were performed using SPSS (Version 22.0) applying non-parametric statistics. In experiment 1, the test fish could predate a maximum of 11 *Daphnia* in each trial (10 of the same species plus one of the other species). In case the test fish would pick the prey randomly, we expect the odd individual to be eaten at the sixth position on average. Thus, a value smaller than six would indicate a preference for attacking the odd individual, while a value larger than six would indicate avoidance of the odd one. Consequently, the obtained points of consumption values were tested against a null-expectation of six using a one-sample Wilcoxon test (Wilcoxon, 1945).

In the social preference experiment, we calculated a preference index by dividing the number of observations *Daphnia* spent in the compartment close to the odour by the number of observations it spent in the odour—and in the tap water compartment combined. Thus, a value above 0.5 indicates a preference for the *Daphnia* stimulus while a value smaller than 0.5 indicates the avoidance of *Daphnia* odours. The obtained preference indices were tested for each species separately (1) comparing the reaction towards the two odour stimuli against each other (*D. pulex* vs. “no odour” vs. *D. magna* vs. “no odour”) using a Mann–Whitney *U* test and (2) comparing each odour treatment separately against a null-expectation of 0.5

using a one-sample Wilcoxon test. Given *p*-values are two-tailed throughout.

3 | RESULTS

3.1 | Predation experiment

In experiment (1a), the *D. magna* was eaten significantly earlier than expected by random choice (one-sample Wilcoxon test: $N = 10$, $Z = 2.913$, $p = 0.004$) in swarms of 10 *D. pulex* and one *D. magna* (Figure 1). In experiment (1b), the *D. pulex* was eaten significantly later than expected by random choice (one-sample Wilcoxon test: $N = 15$, $Z = -2.235$, $p = 0.025$) in swarms of ten *D. magna* and one *D. pulex* (Figure 1).

3.2 | Social preference experiment

In experiment (2a), focal *D. pulex* significantly preferred the side of “no odour” over odour of conspecifics (one-sample Wilcoxon test: $N = 10$, $Z = -2.504$, $p = 0.012$, Figure 2) and over odour of heterospecific *D. magna* (one-sample Wilcoxon Signed-rank test: $N = 10$, $Z = -2.299$, $p = 0.021$, Figure 2). This preference did not differ between the two provided stimulus odours (Mann–Whitney *U* test, $N_{pulex \text{ vs. "no odour"}} = 10$, $N_{magna \text{ vs. "no odour"}} = 10$, $Z = -0.48$, $p = 0.63$).

In experiment (2b), the preference of *D. magna* significantly differed between the two stimulus odours (Mann–Whitney *U* test, $N_{magna \text{ vs. "no odour"}} = 25$, $N_{pulex \text{ vs. "no odour"}} = 19$, $Z = -2.98$, $p = 0.003$,

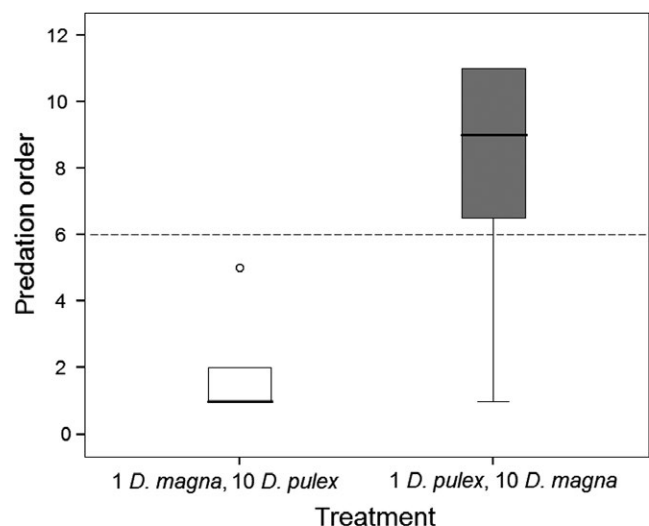


FIGURE 1 Predation experiment. Predation order when three-spined stickleback preyed on either one *D. magna* or one *D. pulex* as the odd animal within a group of ten heterospecifics. A value smaller than six indicates that the odd individual was taken earlier than expected by chance, while a value larger than six indicates that the odd animal was attacked later than expected by chance. Thick black lines represent the medians, boxes encompass the interquartile ranges, whiskers extend to the most extreme data points within $1.5 \times$ the interquartile range outside the box, and the circles show data points beyond the whiskers. In two cases, the odd *D. magna* has been attacked at fifth position

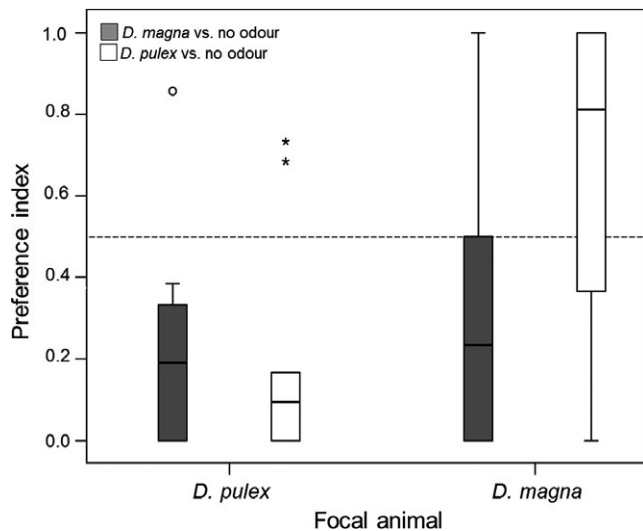


FIGURE 2 Social preference experiment. Preference index of the focal individual for either *D. magna* odour versus “no odour” (grey) or *D. pulex* odour versus “no odour” (white). Preference index values large than 0.5 indicate a preference for the *Daphnia* stimulus, while smaller values indicate the avoidance of *Daphnia* odours. The thick black lines represent the medians, the boxes encompass the interquartile ranges, the whiskers extend to the most extreme data points within $1.5 \times$ the interquartile range outside the box. Circles show data points between 1.5 and $3.0 \times$ the interquartile ranges outside the box, stars indicate data points above $3.0 \times$ the interquartile ranges

Figure 2). Focal *D. magna* significantly avoided the conspecific odour (one-sample Wilcoxon test: $N = 25$, $Z = -2.46$, $p = 0.014$), while they tended to prefer *D. pulex* odour over “no odour” (one-sample Wilcoxon test: $N = 19$, $Z = 1.77$, $p = 0.076$, Figure 2). The latter result, however, failed statistical significance.

4 | DISCUSSION

In this study, we show that larger *Daphnia* are at higher risk of being predated, while overall oddity within a multispecies group had no negative consequences. Interestingly, these differential risks of large *D. magna* and small *D. pulex* were not reflected in their respective social decisions.

Previous studies have demonstrated oddity effects in vertebrates and invertebrates using differently coloured prey items (e.g., Landeau & Terborgh, 1986; Penry-Williams et al., 2018; Ohguchi, 1978). In contrast, such effects are less clear when body size is the odd criterion within a group. For example, both large and small minnows were more likely attacked by predators when they were odd-sized relative to their conspecifics (Theodorakis, 1989), whereas large *D. magna* were generally at greater predation risk independent of group composition (Rodgers et al., 2015). In line with this, large *D. magna* in our study were targeted more often than expected by random choice, independent of being the odd individual (10 *D. pulex*, 1 *D. magna*) or not (10 *D. magna*, 1 *D. pulex*). This suggests that the

oddity effect was overruled by other factors. Many planktivorous fishes preferentially prey on large zooplankton (Holzman & Genin, 2005; Rodgers et al., 2015; Wetterer & Bishop, 1985). This is in accordance with the optimal foraging theory suggesting that predators should maximise their intake of energy and target the most profitable prey (Emlen, 1966; Manatunge & Asaeda, 1998; Mittelbach, 1981; Stephens & Krebs, 1986; Ydenberg, Brown, & Stephens, 2007). Indeed optimising energy intake results in active prey choice in a variety of species. For example, large bluegill sunfish (*Lepomis macrochirus*) and white crappie (*Pomoxis annularis*) selectively chose large *Daphnia* (Manatunge & Asaeda, 1998; Mittelbach, 1981). Similarly, three-spined stickleback in our study chose larger bodied *D. magna*, indicating that they aim at maximal energy intake as well.

If reducing predation risk is the main driver of social decisions in daphnids, it is straight forward to assume that both *D. magna* and *D. pulex* include species identity into their grouping decision. While *D. magna* should show preferences for conspecifics in order to increase predator confusion or risk dilution, *D. pulex* are expected to show stronger preferences for heterospecifics, as they would be the less preferred prey within this group. However, these predictions were not verified in the social preference experiment. Both *Daphnia* species reacted towards the chemical cues, indicating that they are able to recognise the presence of other *Daphnia* using olfactory cues alone. While *D. pulex* generally avoided the odour of other daphnids, *D. magna* showed different reactions towards chemical cues derived from *D. magna* or *D. pulex* and thus use olfactory information in species recognition. *D. magna* significantly avoided cues of other *D. magna*, while they showed a non-significant trend to prefer cues of *D. pulex* over a blank water. Thus, *D. magna* preferred groups in which their predation risk would be increased, leading to the assumption that factors other than predation risk might play an important role in group choice. For example, *D. magna* and *D. pulex* are expected to forage on comparable diets (Hanski & Ranta, 1983). Thus, larger *D. magna* joining a group of *D. pulex* might outcompete these in resource competition due to being able to ingest larger particles, while at the same time enjoy at least some predator protection even in the heterospecific group. Similarly, avoidance of competition might explain the finding that *D. pulex* avoided both cues of con- and heterospecifics. Furthermore, social behaviour of daphnids might be state dependent and be mediated for example by group density, the presence of competitors, hunger level or current predation risk (e.g., Lüring, Roozen, Van Donk, & Gosser, 2003; Roozen & Lüring, 2001). Aggregation preferences and group composition might therefore change over time and depend on contexts (see also Krause & Ruxton, 2002; Shimooka, 2003; Willis & Brigham, 2004). One relevant ecological context is the current predation risk, which can influence grouping decisions (Herbert-Read et al., 2017; Hoare et al., 2004; Jermacz, Andrzejczak, Arczyńska, Zielska, & Kobak, 2017; Kullmann et al., 2008; Pitcher & Parrish, 1993). For example, gammarids (*Gammarus pulex*) only prefer conspecifics when exposed to predator cues (Durieux et al., 2012; Kullmann et al., 2008; Thünken et al., 2010). Similarly, blue mussels (*Mytilus edulis*) form larger groups with increasing predation risk (Reimer & Tedengren,

1997). Especially in *Daphnia*, the effects of predator-derived chemical cues have been shown to influence not only morphology and life history traits, but also behaviour (Boersma, Spaak, & Meester, 1998; Roozen & Lüring, 2001). Consequently, optimal grouping decisions of *Daphnia* under natural conditions might be based on a broad range of many different factors. Such factors shall be elucidated in future studies, for example by simultaneously presenting odour cues of different species or by varying hunger level or current predation risk.

Summarising, we provide insights into the interplay between oddity, optimal foraging and social decisions in aquatic invertebrates. Our results indicate that oddity effects are of low importance in cases individuals differ in nutritional value. Instead, predators optimise nutritional intake. Prey items in turn did not maximise anti-predator protection by choosing the safest group, indicating that aggregations in *Daphnia* are mediated by other factors.

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AUTHOR CONTRIBUTIONS

JGF and TCMB conceived the study; JGF, KL and CJ designed the experiments; SR and KL performed the experiments; SR analysed the data. SR and JGF wrote the manuscript. All authors approved the final version of the manuscript.

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