Prey body size mediates the predation risk associated with being 'odd'

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Running header: Body size and oddity

Abstract

Despite selection pressures on prey animals to maintain phenotypically homogeneous groups, variation in phenotype within animal groups is commonly observed. While many prey animals preferentially associate with size-matched individuals, a lack of preference, or a preference for non-matching group mates is also commonly observed. We suggest that the assortative response to predation risk may mediated by body size, because larger-bodied prey may be at greater risk of predation than smaller bodied prey when in a mixed group due to their greater potential profitability. We test this idea by observing attacks by three-spine sticklebacks *Gasterosteus aculeatus* on mixed groups of large and small *Daphnia magna* prey. We find that smaller *Daphnia* are at greatest risk when they form the majority of the group, while larger *Daphnia* are at the greatest predation risk when they form the minority. Thus, we predict that both large and small prey should benefit by association with large prey, generating a potential conflict over group membership that may lead to the mixed phenotype groups we observe in nature.

Key words: oddity effect, confusion effect, assortment, shoaling, group living.

Introduction

Prey animals across taxa commonly live in groups to reduce predation risk (although other factors such competition, foraging and sociality also contribute to the decision to live in groups; Krause and Ruxton 2002). Choosing to be in a group dilutes individual risk once the group has been detected by a predator (Foster and Treherne 1981), even when the increased attack rate on larger groups is accounted for (Turner and Pitcher 1986). The oddity effect describes how a phenotypically different ('odd') individual in a prey group is at greater risk of predation relative to its group-mates, as it is more easily isolated for attack by a predator (Milinski 1977; Ohguchi 1978; Landeau and Terborgh 1986; Theodorakis 1989). When a group is phenotypically homogeneous, a visual predator suffers from 'predator confusion', reducing targeting accuracy and therefore risk to each prey individual (Neill and Cullen 1974; Landeau and Terborgh 1986; Krakauer 1995), a phenomenon observed in 64% of studies across taxonomic groups (reviewed in Jeschke and Tollrian 2007). Together, the confusion and oddity effects predict that animals should chose to group into homogenous aggregations in which they experience reduced individual risk.

We see this predicted phenotypic uniformity in groups across many species: birds (Smith et al. 2002; Brightsmith and Villalobos 2011; Sridhar et al. 2012), mammals (Meldrum and Ruckstuhl 2009), amphibians (Breden et al. 1982) and fish (Peuhkuri 1997; Croft et al. 2009) assort by body size. Fish in particular have been the focus of many experimental studies providing examples of a preference for associating with similarly sized shoal-mates (banded killifish, Krause and Godin 1994; two-spotted goby, Svensson et al. 2000; swordtails, Wong and Rosenthal 2005; and Trinidadian guppies, Croft et al. 2003). However, variation in body size within groups is still observed (fish shoals: Krause et al. 1998; Hoare et al. 2000; Croft et al. 2009; bird flocks: Farine et al. 2012) and preferences for non-uniformity or the absence of a preference for similarly-sized group-mates have been shown experimentally. In particular, while large-bodied prey fish show preferences for similarly sized conspecifics, small-bodied individuals show either no preference (Svensson et al. 2000; Rodgers et al. 2011) or prefer larger bodied conspecifics (Jones et al. 2010).

One explanation for observations of non-assortment by size is because the assortative response to risk (through oddity) is mediated by body size: differently sized prey exhibit different grouping preferences because their relative risks of being odd differ. Optimal foraging theory predicts that predators should select the most profitable prey (e.g. Stephens and Krebs 1986; Ydenberg et al. 2007), and in the absence of handling constraints associated with larger size, larger-bodied individuals should represent a better meal (Wetterer and Bishop 1985; Manicom and Schwarzkopf 2010). Planktivorous fish preferentially prey on larger forms of zooplankton, which are widely observed to be overrepresented in their diet relative to availability (e.g. Wetterer and Bishop 1985; Li et al 1985). This can be the result of either active choice for particular prey types or reduced encounter rates for small prey due to their smaller size and lower detectability. In many species, however, selectivity for larger-bodied prey is thought to be due to active choice (Li et al 1985; Wetterer and Bishop 1985; Holzman and Genin 2005). Thus, odd prey individuals in a group are likely to be at greater risk of predation when they are large relative to small individuals in a similar oddity situation. In support of this, Peuhkuri (1997; 1998) demonstrated that large fish are more risk averse, reducing foraging when odd in a group, while small fish do not adjust their foraging behavior in response to oddity.

While much work explores the effect of size oddity from the perspective of the prey (i.e. prey behavior and assortment decisions), less is known about how predators balance potentially conflicting predation preferences, and what implications this might have for prey assortment decisions. Classically, Theodorakis (1989) found that both large and small prey individuals were more likely to be attacked by predators (and therefore at greater risk of predation) relative to their group mates when they were odd, but this does not explain the size-mediated shoaling preferences observed in some species (Svensson et al. 2000; Jones et al. 2010; Rodgers et al. 2011). Here, we further explore the interaction between body size and oddity from the predator perspective, asking how important oddity is to predators when active preference for particular body sizes (more profitable prey) may influence their choice.

Methods

Three-spine sticklebacks (*Gasterosteus aculeatus*) preying on *Daphnia* are a classic model for studying confusion and oddity effects (e.g. Milinski 1977; Heller and Milinski 1979; Milinski 1979; Ioannou et al. 2009; Rodgers et al. 2012). Sticklebacks were collected from Saltfleet, Lincolnshire and housed for approximately 1 year in the laboratory before trials began. Fish were housed in groups of 50-150 in large opaque containers at 15°C, on a 12:12h light:dark cycle, and fed daily on defrosted frozen bloodworm (from a commercial aquarium supplier). Fish with body lengths between 35 and 45mm were used in the trials. The prey used in the experiments were *Daphnia magna* of second (small, approximately 1mm) and fifth (large, approximately 2mm) instar sizes (Anderson 1932), purchased from a pet supplies shop in Leeds, UK, collected for sale from ponds in West Yorkshire.

Experiments were based on the protocol detailed in Rodgers et al. (2012), which we summarize here. Externally, at one end of a test tank (20 x 20 x 45cm), we positioned a 3x4 array of *Daphnia* confined individually into transparent 1cm cubes. At the opposite end of the tank, a removable opaque barrier defined an acclimatization zone for the predator (15cm from the tank end), leaving a 30cm attack zone between the barrier and prey. The tank was covered externally on three sides (not including the end where the grid was positioned) with black plastic to minimize disturbance to the fish. Three treatments with different ratios of *Daphnia* sizes were used: 1:11 large:small (large-bodied minority), 6:6 large:small (equal ratios), and 11:1 large:small (small-bodied minority). In the 6:6 treatment prey were arranged with large and small alternating. In the two other treatments, the oddly sized individual was randomly positioned in the grid. We did not observe any size-related differences in the activity of the *Daphnia* when confined in the array.

A test fish was introduced to the acclimatization zone, where it had no visual access to the *Daphnia.* After six minutes acclimatization, the barrier was removed and the stickleback's behavior was filmed using a digital video camera positioned behind the *Daphnia* grid*,* to enable accurate recording of the prey individual first attacked. Once the first attack had been made, the trial finished and the test fish was removed. Fish that had not made an attack within 10 minutes of the barrier being removed were excluded from the experiment. We recorded 16/30 successful attacks in the 1:11 (large:small) treatment, with 18/28 and 19/44 on the 6:6 and 11:1 treatments respectively. Of those that did not attack, 17 fish did not emerge from the acclimatization zone, and 29 emerged but did not attack. Three other trials were discarded due to failures in the recording. The water in the test tank was changed between each trial to control for olfactory cues from previous test fish. No olfactory cues from the *Daphnia* were available to the predators. Each fish was used only once then returned to the stock tanks. *Daphnia* were returned to a size-matched pool for reuse in subsequent trials.

All statistical analyses were carried out using R v. 2.10.1 (R Development Core Team 2007). Exact binomial tests were used to test for prey body size preferences of sticklebacks. Expected proportions of attacks on large individuals (assuming random predation) were dependent on the distribution of body sizes within the group. In the 1:11 large:small treatment, we would expect the predator to target the large individual in 1 in every 12 trials, giving an expected proportion of 0.083. Expected proportions for the 6:6 and 11:1 large:small treatments were 0.5 and 0.917 respectively. Estimates of 95% confidence intervals for the observed proportions were calculated using the ‘modified Wald’ method (Agresti and Coull 1998). For illustrative purposes, we then converted the attack data into per capita predation risk for both large and small individuals. If a group consisted entirely of size-matched *Daphnia* (N=12), the per capita risk for each individual would be 0.0833 (=1/12). We calculated the per capita risk for each group composition as the proportion of trials in which an individual of the size under consideration was targeted, divided by the number of individuals of that size in that trial (Rodgers et al. 2012).

Results

The number of times the predator targeted the large individual was significantly higher than random expectation in the equal ratios treatment (6:6 large:small, large individual targeted in 17/18 trials, p<0.001). The large individual was also preferentially targeted in the large-bodied minority trials (targeted in 4/16 trials, p=0.039) but the small individual was not preferentially targeted where it was in the minority (large individual targeted in 19/19 trials, p = 0.399, figure 1a). Thus, predators target large individuals more often than expected by chance when grouped with a higher or equal number of small individuals. When a group of predominantly large prey includes a single small individual, predators attack both large and small prey at a rate consistent with random expectation (although the small individual was never attacked in this treatment this is not statistically distinguishable from random attack).

We next calculated the per capita predation risk for large and small individuals for each of the group compositions tested (figure 1b). Per capita risk for large individuals is greatest when they form the minority of the group, and decreases as the number of large individuals in the group increases. For small individuals, absolute per capita risk is always lower than for large ones, and they are also at greatest per capita risk when there is a single large prey in the group, and their risk decreases as the number of large individuals in the group increases (figure 1b).

Discussion

Here we have shown that large prey are at consistently greater risk of attack than small prey when in mixed groups, and that the risk of attack by a predator changes according to the composition of the group. For large prey, risk is greatest when it is in the minority in the group. For small prey, however, being odd in a group does not translate into increased risk – here, all observed attacks were on large individuals and attack rates were consistent with random attack. Small prey have greater per-capita risk when they form the majority of the group, and lowest risk when make up a smaller proportion. This contrasts with the work of Theodorakis (1989), who found that both large and small individuals were preferentially targeted, and suggests that the oddity effect alone does not explain predation risk in our system. Instead, our results may be consistent with a preference for more profitable, larger bodied prey (Wetterer and Bishop 1985; Li et al. 1985; Holzman and Genin 2005; Stephens and Krebs 1986; Ydenberg et al. 2007) and this may override any confusion and oddity effects (which are known to operate in the stickleback-*Daphnia* system; Milinski 1977; Heller and Milinski 1979; Milinski 1979; Ioannou et al. 2009; Rodgers et al. 2012).

If predation risk is greater on larger individuals, and confusion effects operate in a particular system, we would expect that predation pressure should lead to social preferences that minimize risk, that is, assortment with large individuals for both large- and small-bodied prey, a pattern observed in fish by Jones et al. (2010) and supported by Peuhkuri (1997) and Rodgers et al. (2011), but in contrast to Lachlan et al. (1998) who observed the opposite pattern. Our results also contrast with those of Theodorakis (1989) who found that both large and small odd prey were preferentially targeted by fish predators. If both large and small individuals can reduce risk by assorting with large conspecifics, this generates a potential conflict between the two. Large individuals would benefit by excluding or avoiding small individuals from their groups, while small individuals benefit from joining those groups. It may be costly to exclude group members, particularly in free-entry groups such as fish shoals (Krause and Ruxton 2002) resulting in the mixed phenotype groups that we observe in nature (Tosh et al. 2007; Rodgers et al. 2012). Equally, there may be reasons other than predation why individuals do not appear to assort by phenotype. In shoaling fish, familiarity (Griffiths 2003; Ward and Hart 2003), recent shared experience of particular habitats, mediated by olfactory cues (Ward et al. 2005), foraging competition (Metcalfe and Thomson 1995), nutritional state (Morrell et al. 2007) and crypsis relative to the environment (Rodgers et al. 2012) all contribute to social decision-making and may lead to non-assortative behavior.

Optimal association behavior may also be constrained by other factors. In mobile species with fission-fusion dynamics, moving between groups may be common (Croft et al 2003; Couzin 2006; Sueur et al 2011) allowing preferences to be expressed, but in other species, aggregations may simply occur where environmental conditions are favourable, rather than through social choice, leading to non-assorted groups. In contrast, in groups with defined social structures, such as dominance hierarchies, these structures may constrain the freedom to select optimal associates. For example, in mixed-species flocks of tits (Paridae), subdominants are limited in their interactions in a group, and do not flock with similarly sized heterospecifics, as might be predicted (Farine et al 2012).

From the predator’s perspective, selection of odd individuals would overcome the confusion generated by groups of moving prey (Neill and Cullen 1974, Ohguchi 1978; Landeau and Terborgh 1986, Krakauer 1995), carrying with it both short and longer-term fitness benefits (as well as increased attack success, the reproductive performance of goshawks *Accipter gentilis* increases with their selectivity for rare colour morphs of feral pigeons *Columbia livia,* for example (Rutz 2012)). However our experiments show that predators do not always select these odd individuals. Given a choice of equal numbers of both prey types, predators selected the large prey in almost every case, suggesting that large prey are preferred, potentially because they are nutritionally more valuable. Observations suggest that for larger sticklebacks, as used in our experiment, handling time even for larger *Daphnia* is likely to be negligible (Gill and Hart 1994), and so larger *Daphnia* (which likely contain 2-4x the energy content of small Daphnia; Nuutinen and Ranta 1986) are very likely to be more profitable, reflecting the widespread observation that larger zooplankton are preferred by planktivorous fish (Wetterer and Bishop 1985, Li et al. 1985) resulting from active choice for more profitable prey (Wetterer and Bishop 1985; Li et al. 1985; Holzman and Genin 2005). Predators are therefore trading off the potential benefits of a better meal against the reduced chance of success resulting from confusion effects (Krakauer 1995; Ioannou et al. 2007). We assume that large odd prey may be preferentially targeted because predators benefit from both avoiding confusion and capturing a valuable target, but when small prey are odd, the benefits of using oddity to overcome confusion are not balanced by the lower nutritional value of the target prey. However, the increased conspicuousness of large odd prey is also likely to play a role in predator targeting decisions (Rodgers et al. 2012), potentially reducing the effectiveness of dilution effects for these prey.

But why was the large prey individual not always attacked? Both optimal foraging for more profitable prey and oddity effects would predict that the large individual should always be preferred when in the minority, and although we found a significant preference, in 75% of trials where the large individual was odd, a small individual was attacked. One explanation may be that predators were unable to accurately distinguish between large and small *Daphnia* in our experimental set up, but the targeting rates of large prey in the equal ratios treatment suggest that this was not the case, and predators could accurately distinguish the large individual. Secondly, sticklebacks may not have been able to simultaneously view all prey, and were selecting from among a subset, reflecting a pattern of sequential rather than simultaneous encounter of prey types (see Stephens and Krebs 1986), which would predict that small individuals would be attacked if large ones were not available at that time. Planktivorous fish are able to detect and attack prey within around 60° of either side of their heads (e.g. Flore et al. 2000; Asaeda et al. 2002; Cobcroft and Pankhurst 2006) which would suggest that they are able to view the complete prey grid from the majority of locations within the tank (only by approaching closer than 2cm would the angle subtended by the group exceed 120°), and our prey group was within the range of *Daphnia* configurations of previous confusion and oddity papers (Heller and Milinski 1979; Milinski 1979; Ioannou et al. 2009; Rodgers et al. 2012). We did not quantify reaction distances in our experiment, but Ioannou et al. (2011) indicate that sticklebacks will attack groups of prey from distances of up to 40cm, with a mean reaction distance of approximately 180mm. Thus, it seems likely that all prey could be viewed simultaneously, and attacks began when this was the case.

Finally, attacking swarming prey requires additional cognitive attention, which must be redirected from other activities, particularly anti-predator vigilance (Milinski and Heller 1978), potentially placing the predators themselves at increased risk of predation. A predator must therefore balance these conflicting demands in selecting which individual(s) from an aggregation to attack, and a small individual may be targeted even when a larger one is available. Our results demonstrate that oddity effects interact with other individual and group characteristics, and these complex interactions are likely to shape prey choice decisions for predators, as well social decisions and patterns of assortment by prey in both laboratory trials and free-living populations.

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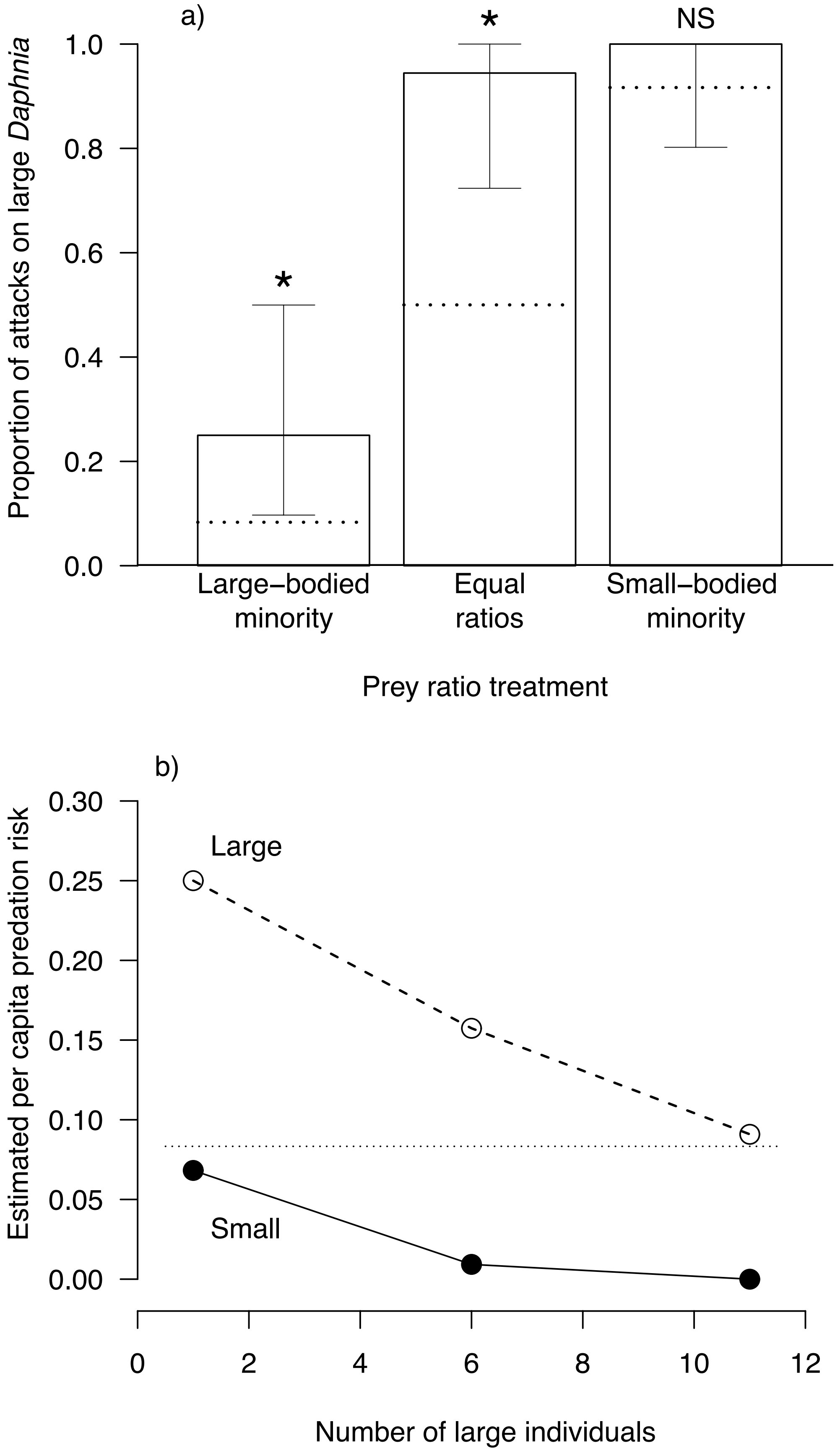
Figure Legends

Figure 1 a) Proportion of trials resulting in predator attacks on large *Daphnia*, for each of the three prey group compositions (ratio of large:small individuals for each treatment are as follows: 1:11 large-bodied minority, 6:6 equal ratios, 11:1 small-bodied minority). Error bars represent 95% confidence intervals calculated using the ‘modified Wald’ method described in Agresti and Coull (1998). Dashed horizontal lines show the proportion expected by random prey selection, according to the prey group composition. Significant differences between observed proportions and random expectation are shown with an asterisk. **b)** Estimated per capita predation risk for large (open circles, dashed line) and small (filled circles, solid line) individuals as a function of the number of large individuals in the group, calculated from the attack data shown in a). The horizontal dotted line represents the per-capita risk to each individual in a uniform group of 12. Lines connecting points are for illustration only.


a)
Proportion of attacks on large *Daphnia*
1.0
0.8
0.6
0.4
0.2
0.0
*
*
NS
Large–bodied minority
Equal ratios
Small–bodied minority
Prey ratio treatment
b)
Estimated per capita predation risk
0.30
0.25
0.20
0.15
0.10
0.05
0.00
Large
Small
0
2
4
6
8
10
12
Number of large individuals