

The Effect of Prey Density on Predators: Conspicuousness and Attack Success Are Sensitive to Spatial Scale

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ABSTRACT: In contrast to the numerous studies that have examined the response of predators to prey group size, little is known about how prey density affects prey detection and the accuracy of attacks. We demonstrate that increasing the density of *Daphnia magna* swarms increases conspicuousness to a natural predator, the three-spined stickleback. Denser areas of groups were more conspicuous, as the fish attacked prey in denser parts of the group than would be expected if they attacked the nearest prey upon entering the feeding chamber. The spatial error of attacks also increased with the density around the target; hence, different stages of predation (searching for vs. successfully attacking prey) seem to select for opposing responses to prey density. However, whereas the effect of density on target selection only occurred using a global measure of density (average interindividual distance), the effect on attack error was only significant using a local measure of density (Voronoi polygon area). We believe this effect of spatial scale reflects the reduction in the number of prey in the visual field of the predator as an attack progresses, providing a perceptual basis for the importance of spatial scale in density-dependent processes.

Keywords: *Daphnia*, domain of danger, conspicuousness, selfish herd, spatial scale, three-spined stickleback.

Introduction

The spatial distribution of individuals relative to one another is a trait under major selective pressure in both plants and animals and has led to a wide range of morphological and behavioral strategies to facilitate dispersal from, or aggregation toward, conspecifics (e.g., Strong 1988). Predation risk in particular has been shown to be an important factor in driving spatial relationships between animals, affecting both the formation of groups and the pattern of spacing within groups (Krause and Ruxton 2002). Although group size (the number of individuals in a group) has attracted the vast majority of theoretical and empirical

attention when considering the effect of spatial distribution on predator behavior (Krause and Ruxton 2002), prey density (the spatial proximity of individuals to one another) may also affect prey detection, target selection, and attack success. Since density, not group size, has held prominence in our understanding of ecological processes from the classical models of Lotka-Volterra (Lotka 1925) onward, how predation responds to prey density at a behavioral level is essential to explaining why predator-induced mortality varies with density.

Little is known about how the density of prey affects conspicuousness to predators (Jackson et al. 2005). The greater visual angle produced by larger group sizes has formed the mechanistic basis for theoretical work on group detection rates (Vine 1973; Treisman 1978). These models assume that spacing between individuals remains constant, so that the dimensions of the group are directly related to group size. In the majority of animal groups, this is not the case, since interindividual distances vary with spatial position in a group (Bumann et al. 1997) and over time (Magurran and Pitcher 1987; Morrell and Romey 2008). Although spacing within groups is clearly important to prey, how this affects detection of the group remains largely untested. Using humans searching for static, computer-generated prey, Jackson et al. (2005) demonstrated a positive effect of group size on the detection of cryptic prey but no density effect. Moreover, to our knowledge, no theoretical model directly considers an effect of density on conspicuousness. This is likely to be due to the difficulty of modeling visual processing beyond a simple visual angle approach, and visual angle may be shown to be an inadequate model if group compaction increases detection rate.

The selfish herd model (Hamilton 1971) is often cited to explain the formation and compaction of animal groups. The key assumption is that the predator can appear anywhere in the environment and targets the nearest prey; thus, the area around an individual nearer to it than to any other individual (the Voronoi polygon area; Viscido

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and Wethey 2002) is proportional to its relative risk of predation (its “domain of danger”). To minimize this area, individuals move toward one another, forming groups (Hamilton 1971). However, even though attacking the nearest prey may be more likely to result in a successful attack since the prey has less time to react (as demonstrated in Cresswell and Quinn 2004), limitations of knowledge on prey positions may stop this occurring. When predators have to actively search for prey, factors other than proximity, such as the ease of detection, may affect which prey is targeted (Stankowich 2003). If greater densities of prey within groups are more conspicuous, individuals in a compact part of the group may actually be at greater risk than spatially isolated individuals. There is some evidence that denser parts of groups are more conspicuous, since three-spined sticklebacks (*Gasterosteus aculeatus* L.) initially attacked dense parts of *Daphnia* swarms when the prey were cryptic but initially attacked strays when the prey were conspicuous (Milinski 1977). This sensitivity to prey coloration rules out a preference for dense prey to maximize feeding rates, since density had a positive effect on attracting initial attacks only when the prey were harder to detect.

More attention has been given to the effect of prey density on the postdetection phase of predation. The confusion effect describes a reduced rate or success of attacks on prey groups as multiple targets overload the information-processing capacity of predators (Krakauer 1995). The effect has been shown to increase with the density of prey, independently of group size, leading to a preference for spatially isolated individuals (Milinski 1977). However, other experiments have failed to observe an effect of density both with fish using attack rate (Ioannou et al. 2008) and with humans measuring the time taken to make an attack and attack success (Ruxton et al. 2007). This disagreement may be due to density being varied over different spatial scales in the different experiments; for example, only increases in the local space around a prey may affect predatory confusion. In addition, different response variables were used to assess the confusion effect in the different studies (Ioannou et al. 2008).

These points illustrate that whereas denser prey may be more conspicuous to predators, isolated individuals may be encountered first (the selfish herd) and/or be attacked with more success (the confusion effect). Hence, the optimal response of a predator to prey density, and the optimal density for prey, is unclear and may vary with the stage of predation. This has been shown to occur with the group size of prey, since although larger group sizes may be more conspicuous to a predator (Ioannou and Krause 2008), the success of attacks may decline as a result of the confusion effect (Cresswell 1994). We predict a similar trend for prey density: denser prey may be more con-

spicuous, but this may be compensated for by a reduced success of attacks.

Using the three-spined stickleback–*Daphnia magna* predator-prey system, we conducted three experiments to examine the effect of prey distribution on progressive stages of the predation cycle (Lima and Dill 1990): the detection of prey, targeting of an individual, and attack success. We used a three-treatment design to determine whether the number of prey, the area occupied by the group, and/or the density of individuals has the effect on detection rate normally associated with increased group size. To control for increased per capita activity in larger groups (Grand and Dill 1999), which can increase conspicuousness (Krause and Godin 1995), we examined whether the distance between isolated prey affected detection rate. We then investigated whether any effect of prey density on detection rate also applies to the targeting of individuals from within a group and whether this is affected by group size. The relative importance of prey distribution on conspicuousness versus a selfish herd effect was assessed, measuring prey spacing at both local (Voronoi polygon area) and global (average interindividual distance) spatial scales. These measures of spacing were then used to determine the effect of prey density on the spatial error of attacks, which is negatively related to attack success (Ioannou et al. 2008).

Method

The general procedure was to present groups of *Daphnia* to habituated, naive, and hungry sticklebacks. Because we have used this approach before (Ioannou and Krause 2008; Ioannou et al. 2008), and for brevity, we present a summary of the methods here, with the full, detailed methods available in the appendix in the online edition of the *American Naturalist*.

Daphnia were used as a model prey organism because their behavioral responses to predation risk have been demonstrated repeatedly, with fish odor cues leading to compaction of *Daphnia* swarms (Pijanowska 1994), vertical migration (Watt and Young 1994), and uniformity between individuals in swimming speed (Jensen et al. 1998). Moreover, these responses have been shown to have adaptive value by examining the response of predators to *Daphnia* aggregation and uniformity, with benefits from attack abatement (Jensen and Larsson 2002) and confusion effects (Milinski 1977). In fact, the functional response of predators feeding on *Daphnia magna* swarms suggests group level as well as individual benefits to aggregation (Young et al. 1994).

In all experiments, 35 three-spined sticklebacks were habituated overnight to tanks split into two areas connected by an opening: a living area and a smaller feeding

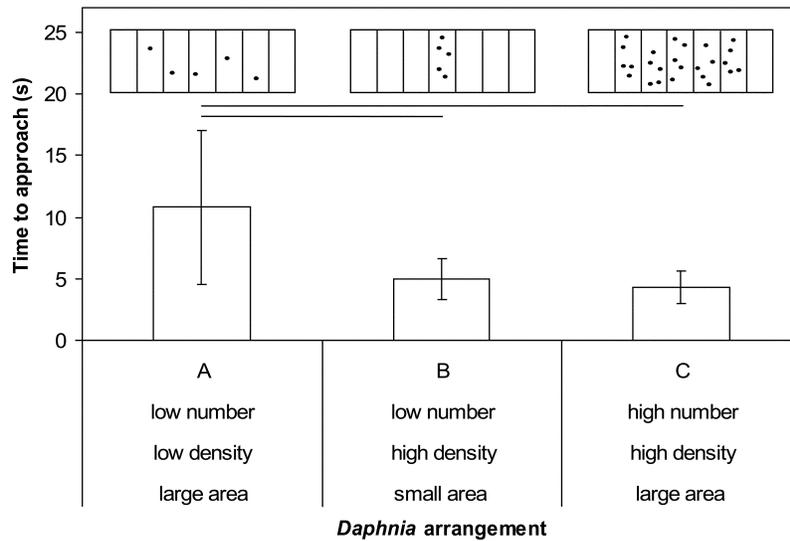


Figure 1: Effect of prey distribution on detection rate, measured as the time taken to approach the prey. Significant differences in detection rate between treatments are indicated by horizontal lines above the bars ($P < .05$). Means are shown with 2 SEs.

area, where the fish were fed the evening before testing. The fish were able to explore both areas during habituation. Before testing, all fish were moved into the living area, and the *Daphnia* treatments were set up in glass containers on the wall of the feeding area opposite the opening. Fish entering the feeding area were observed without disturbance and were removed once the prey was approached and attacked. Removed fish were replaced at the end of each day.

The first experiment presented *Daphnia* in test tubes in one of three configurations to determine the separate effects of group size, density, and area on conspicuousness: A: 0, 1, 1, 1, 1, 1, 0 (low number and low density with large area); B: 0, 0, 0, 5, 0, 0, 0 (low number and high density with small area); C: 0, 5, 5, 5, 5, 5, 0 (high number and high density with large area). The time taken to approach the *Daphnia* (defined as an orientated approach to prey within one body length) was recorded, with 28 trials carried out for each treatment.

To control for possible interactions between *Daphnia* individuals within a test tube, we repeated the procedure above using the same apparatus, with prey presented as either a clumped, high-density treatment (0, 1, 1, 0, 0, 0, 0) or a separated, low-density treatment (0, 1, 0, 0, 0, 1, 0). Prey were isolated from one another in both treatments. The same two *Daphnia* were used in paired trials of the two treatments to control for inter-*Daphnia* variability. Thirteen such pairs of treatments were carried out.

In a previous study, we demonstrated an effect of prey

group size on targeting error (the distance from a strike to the nearest prey), which was used as the mechanism to explain why attack success declined with increased group size in another experiment (Ioannou et al. 2008). The video footage and data from this previous study have been reanalyzed here to examine whether prey distribution within groups affects the selection of a target from the group.

Prey were presented in a 10 × 10-cm glass chamber with an internal width of 4 mm, which compacted the swarm into two dimensions. As the fish approached the group from the third dimension, the effect of edge individuals being encountered and detected first was minimized (Romney et al. 2008). Group sizes of 5 (21 trials) or 20 (20 trials) were presented to the fish. The approach and attack were recorded using a digital camcorder facing the feeding area, from which the still image of the first attack was determined. Coordinates of each *Daphnia* allowed us to calculate the spacing around each individual at two spatial scales: a local scale that is equivalent to Hamilton's (1971) domain of danger (Voronoi polygon area [VPA]) and a global scale that uses information on all other individuals in the group (average interindividual distance [IID]).

The spacing of the *Daphnia* nearest the fish's mouth relative to the rest of the group was calculated as relative spacing of target = spacing of target/median spacing of group, using both local and global measures of spacing. This was compared with the relative spacing of the nearest prey to the fish when it first entered the feeding area (and was naive to the presence of prey). Mixed models were

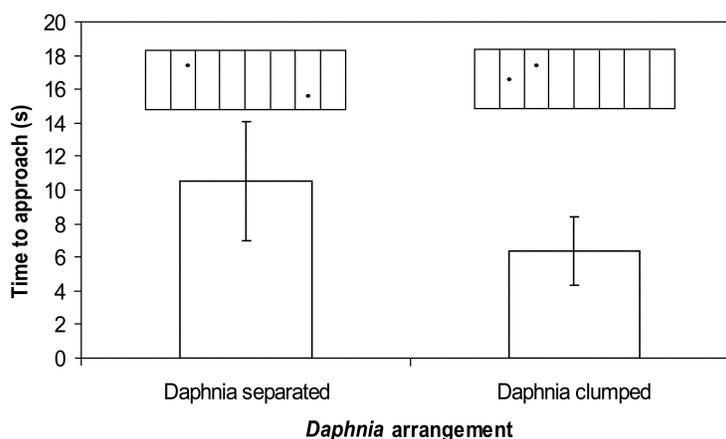


Figure 2: Effect of distance between two isolated prey on detection rate, measured as the time taken to approach the prey. Means are shown with 2 SEs.

used to determine the effects of group size and phase (enter or attack) on the relative spacing of the prey nearest the fish, with trial as a random factor. Finally, the effect of prey density on targeting error was also examined by analyzing the distance from the attack to the nearest prey as a function of target spacing (using both the VPA and IID).

Results

The physical properties of *Daphnia* groups (number of prey, density, and/or the space taken by the group) had a significant effect on conspicuousness, with a significant overall difference between treatments in the time taken for the fish to approach the prey (fig. 1; generalized linear model with negative binomially distributed errors, log-likelihood ratio test $[LRT]_{2,81} = 21.86, P < .0001$). There was no significant difference in approach time between the two treatments where density was held constant but number and area varied (C vs. B; $z = 0.64, P = .52$). However, there was a significant increase in the time taken to approach when the group was less dense, relative to both a dense group occupying a smaller area (A vs. B; $z = -3.56, P < .0005$) and a more numerous group occupying the same area (A vs. C; $z = -4.18, P < .0001$). Thus, density had the only effect on approach time, with approach time declining with increasing density of the group rather than with the number of individuals or the spatial extent of the group. Correspondingly, clumped isolated individual prey (i.e., prey at high density but unable to interact) were approached significantly sooner than separated individual prey (fig. 2; paired t -test, $t = 3.2, df = 12, P < .01$).

We then examined whether individuals in more or less compact regions in a group are more likely to be attacked.

Although the two relative measures (VPA and average IID) were positively correlated when all data were pooled (Spearman's rank, $r_s = 0.50, n = 78, P < .001$), there was enough variation to give quantitatively different results when examining the effect of relative spacing. When using a local measure of spacing (the VPA), the prey nearest the fish in a group of 20 occupied a significantly less dense part of the group than in a group of 5 (fig. 3A; mixed model, $F_{1,37} = 27.04, P < .0001$). However, there was no significant change in relative spacing from the nearest prey on entering the feeding area to the prey that was attacked; that is, local density had no effect on targeting prey ($F_{1,38} = 0.96, P = .33$). In contrast, when using a global measure of density (average IID), the fish targeted prey in significantly denser parts of the group than the individual they were nearest at the moment of entering the feeding area (fig. 3B; mixed model, $F_{1,38} = 11.69, P < .005$). There was no significant effect of group size using this measure of spacing ($F_{1,37} = 3.33, P = .08$).

Because relative spacing at the two spatial scales was highly correlated, the measures of spacing were reduced to a single principal component, measuring overall relative spacing, in a principal components analysis. The prey nearest the fish was in a relatively less dense part of group size 20 compared with group size 5 (mixed model, $F_{1,37} = 15.92, P < .0005$). The fish also targeted prey from denser regions of the group than the region they were nearest to when first encountering the prey ($F_{1,37} = 7.04, P < .05$). No interactions in any of these analyses were significant ($P > .05$).

Targeting error was significantly reduced as the VPA of the target prey became larger (fig. 4; linear model, $F_{1,39} = 5.49, P < .05$). The average IID of the target, how-

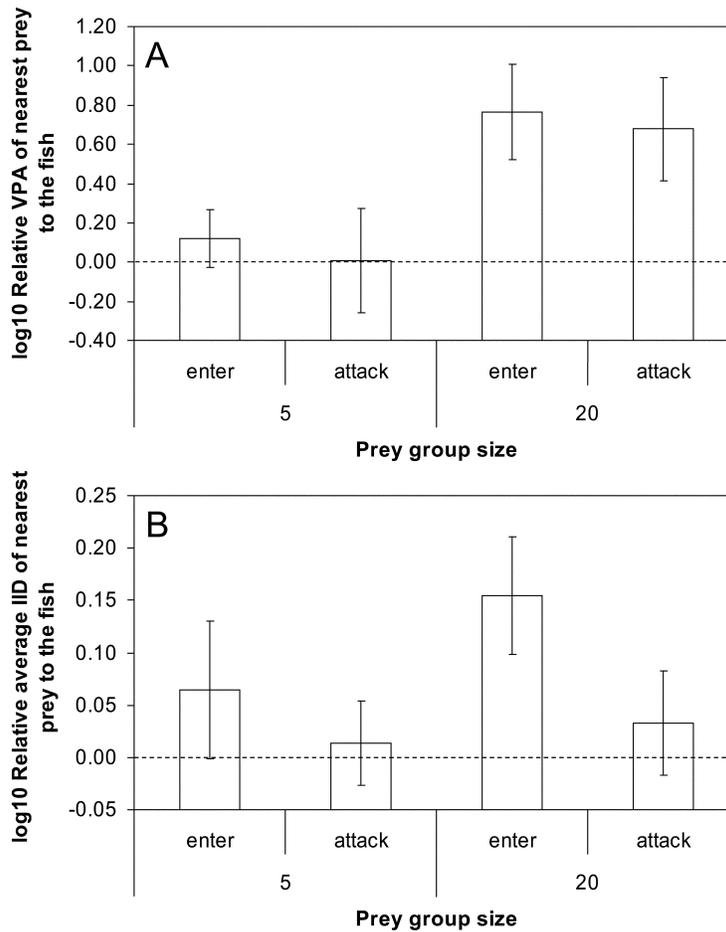


Figure 3: Spacing (mean \pm 2 SE) of the prey individual nearest to the fish, relative to the median spacing of the group. “Enter” refers to the spacing of the prey nearest the fish on entering the feeding area, and “attack” refers to the relative spacing of the individual actually targeted. Spacing was quantified at two spatial scales: a local scale (Voronoi polygon area [VPA]; A) and a global scale (average interindividual distance [IID]; B). Dashed lines mark the median spacing in a group.

ever, had no effect on the spatial error of attacks ($F_{1,39} = 0.61$, $P = .44$).

Discussion

The density of *Daphnia* had a significant effect on multiple stages of predation by sticklebacks. Denser groups appeared to be more conspicuous, as were denser areas within groups, leading to the increased targeting of individuals in denser parts of the group than would be expected if the predator targeted the nearest prey. However, targeting error increased as the targeted prey distribution became denser. It appears, therefore, that prey density selects for different responses from the predator at different stages of an attack, since denser prey are more easily detected but are attacked with less accuracy. This resonates

with the effect of redshank (*Tringa totanus*) flock size on sparrowhawk (*Accipiter nisus*) and peregrine (*Falco peregrinus*) predation, where larger groups were preferentially attacked but the success of attacks was greater on smaller flocks (Cresswell 1994). The same trend was found by Krause and Godin (1995) with acara cichlids (*Aequidens pulcher*) predating guppy (*Poecilia reticulata*) shoals. The net intake of a predator may be maximized by frequent but relatively unsuccessful attacks on easily found prey. Although the invertebrate prey of sticklebacks are relatively immobile, which allows the fish to make multiple attacks on a prey individual, unsuccessful attacks can lead to the prey being consumed by conspecifics since sticklebacks are often involved in scramble competition. Optimal responses to prey distribution will depend on the difficulty in finding prey versus the cost of launching unsuccessful

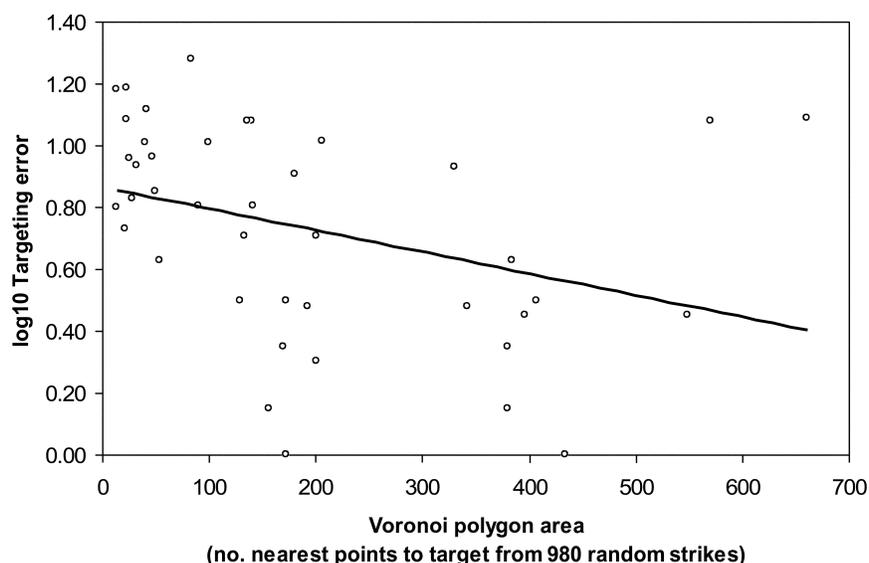


Figure 4: Effect of prey local spacing on the targeting error of attacks, measured as the distance from the strike to the nearest prey. Solid line is from a linear regression.

attacks and may explain the large variation between predators in the frequency and success of attacks (Curio 1976).

In our study, however, the apparent conflict between detecting and successfully attacking prey was further complicated by spatial scale: the effect of density on conspicuousness occurred only at a global measure of spacing (average interindividual distance), while the effect on targeting error was evident only at a local measure of spacing (Voronoi polygon area). A possible explanation lies in the number of prey present in the visual field of the predator at different stages of preying a group. Generally, a predator will detect a group at a distance, where a relatively large number of prey individuals will be in the visual field. At this stage, the detection of a particular prey individual will be influenced by more than just its nearest neighbors, and hence a large spatial scale of density will be appropriate. However, after approaching the group to launch an attack, the number of prey in the visual field will be greatly reduced, and only the local neighbors of the target prey will be visible to influence attack success via the confusion effect. The importance of spatial scale has been ignored by models of detection rate, target selection, and attack success, although it makes intuitive sense that the view a predator perceives changes as an attack unfolds.

There are few studies on predator-prey behavior that have examined the effect of spatial scale, even though, for example, it may explain why some studies have found an effect of prey density on the confusion effect (Milinski 1977) whereas others have not (Ruxton et al. 2007; Ioannou et al. 2008). A reason for this may be that the im-

portance of spatial distribution in behavioral predator-prey studies has focused on prey group size (Krause and Ruxton 2002), where the group is easily defined by sharp boundaries and does not vary with spatial scale. In contrast, ecologists dealing with population density do not often have this luxury and have recognized the importance of spatial scale in plant and animal ecology for some time (Ives et al. 1993). For example, spatial scale has effects on the relationship between host density and parasitoid aggregation (Heads and Lawton 1983) and also plant density and slug herbivory (Gunton and Kunin 2007). In fact, our results suggest a perceptual mechanism for a spatial scale effect on density-dependent predator-induced mortality and, hence, a behavioral basis for the importance of spatial scale in population and community dynamics. The importance of spatial scale in our study demonstrates that even methods for measuring spacing based on detailed spatial data may not be suitable to reveal effects on both prey detection and the success of attacks simultaneously. Examining effects at multiple spatial scales is clearly required, and where this is not possible, the scale most appropriate to the hypothesis being tested should be used.

Existing theory on the effect of spatial distribution on detection rate—that is, the greater visual angle produced by larger groups (Vine 1973; Treisman 1978)—cannot explain why denser prey were more conspicuous. As the density within a group increases, the visual angle either declines (if the visual angle is produced by the boundaries of the group) or remains constant (if it is the sum of the angles produced by all group members). This assumes that

the whole prey group is within the visual field of the predator, and our experiments were designed to present all the prey to the predator simultaneously. However, it has been shown that the focus of attention can be a small subset of the total visual field when searching for cryptic prey (Dukas 2002 and references therein), which could explain the observed effect of prey density within a visual angle framework. When prey are at a low density, few will be within the limited focus of attention at any one time, producing a small visual angle and hence low detection rates. In contrast, a large visual angle will be produced when prey are dense, since numerous prey will fall within the focus of attention.

As predicted by Hamilton (1971), the fish tended to be nearest prey that occupied less dense parts of the group when first encountering the prey, which was true for both global and local measures of individual spacing. This was especially pronounced at group size 20, probably as a result of greater variation in the spacing of prey individuals compared with smaller groups. At least at a local measure of spacing, this led to the targeting of prey in less dense areas, in agreement with Hamilton (1971).

How does the influence of prey density on predators affect the optimal spacing strategy for prey? Prey may face a trade-off in the optimal spatial position (as with optimal group size; Krause and Ruxton 2002) since densities will often be positively correlated across spatial scales (Gunton and Kunin 2007). However, although there was a shift to attack denser prey than expected, violating Hamilton's (1971) key assumption, the selfish herd effect was not completely negated. The net effect of these two opposing mechanisms (conspicuousness and the selfish herd) was that prey at median densities were actually targeted, rather than the prey in the most dense areas. This selfish herd effect was in addition to the benefit of reduced attack success when the predators attacked denser prey. Additionally, knowledge of the spatial positions of other prey within groups will often be limited to nearest neighbors (Ballerini et al. 2008), and furthermore, the encounter dilution effect (Watt et al. 1997; Jensen and Larsson 2002) should still presumably apply to prey in dense patches as well as in large groups. Minimizing the domain of danger is likely to be the most effective strategy to reduce overall risk, and these factors can explain group compaction as a widespread response to predation (minnows [*Phoxinus phoxinus*]: Magurran and Pitcher 1987; tadpoles [*Bufo bufo*]: Watt et al. 1997; fiddler crabs [*Uca pugilator*]: Viscido and Wethey 2002).

This study considered the spatial distribution of prey at relatively small spatial scales, specifically, the scale within the visual field of the fish. At landscape scales, however, prey distribution will also affect the rate of encounter between predator and prey, a phase of predation ignored in

the current study. In this case, prey may become more evenly distributed in response to predators when both predators and prey are free to move (Lima 2002 and references therein). This suggests that under the threat of predation, there may be a transition from aggregated to even prey distributions as spatial scale increases.

The perceptual constraints of predators drive the effect of density on conspicuousness and also an effect of spatial scale. A formal model of these ideas based on visual processing, as well as further experimental studies, is required to confirm these proposed mechanisms. Presumably, the visual processing of predators evolved to maximize prey intake at minimum cost, and theoretical studies could determine the optimality of the visual system to different prey distributions and environmental conditions. Since the prey themselves are also under selection, coevolution between the predator's visual system, and the spatial distribution of prey, determined by behavior, seems likely.

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