

# Do 3-D predators attack the margins of 2-D selfish herds?

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To explain the evolution of grouping, Hamilton's selfish herd theory assumes that predators attack the nearest prey and that both are acting on a 2-dimensional (2-D) plane. This proximity assumption in his theory is one explanation for marginal predation, the phenomenon whereby predators attack peripheral members of a prey group. However, in some ecological circumstances, predators move in 3-dimensional (3-D) space and prey in 2 dimensions. Because a predator coming from above or below the group may have relatively equal access to all members, marginal predation cannot be assumed. In this paper, we test whether marginal predation occurs in such a 3-D/2-D geometry. We carried out 3 controlled laboratory experiments in which fish attack prey grouped at the water's surface. Predators were bass (*Micropterus salmoides*) or goldfish (*Carassius auratus*), and prey groups were either free-swimming whirligig beetles (*Dineutes discolor*) or a constrained group of tadpoles (*Bufo bufo*). In all 3 experiments, predators were significantly more likely to attack the periphery of prey groups. Our experiments also show that marginal predation is robust to differences in overall density within a prey group and that the fish are not reacting to observable state or behavioral correlates to position within a prey group. Furthermore, our results showed that predators will attack group margins even when there is no variation, due to position, in nearest neighbor distance. *Key words*: attack preference, grouping, marginal predation, predator-prey geometry, selfish herd. [*Behav Ecol* 19:74–78 (2008)]

There are a number of hypotheses for why animals group (Krause and Ruxton 2002). One of the most cited is the selfish herd hypothesis (Hamilton 1971) in which prey attempt to position themselves so that there is another member of their group between itself and a predator that is assumed to emerge randomly within the group and attack the nearest prey. Vine (1971) developed a model for predators attacking the nearest target from outside the group. Taken together, these 2 models predict peripheral predation (synonymous with "marginal predation," reviewed in Krause 1994). However, nearly all research, both theoretical (Williams 1964; Hamilton 1971; Vine 1971; Viscido and Wetthey 2002) and experimental (reviewed by Krause 1994 and Stankowich 2003), has focused on animals in which predators move on a 2-dimensional (2-D) plane approaching prey groups that occupy the same plane. Similarly, marginal predation has been shown for predators that move in 3-dimensions (3-D) preying on 3-D groups (Krause 1994), such as fish attacking the periphery of *Daphnia* swarms (Jakobsen and Johnsen 1988) and wasps and hummingbirds attacking the periphery of spider groups (Rayor and Uetz 1990). However, central predation has been documented in some species, especially when the prey group is very numerous or when the predator is fast and/or cooperates with other predators (Parrish 1989; Parrish 1992).

Despite this broad theoretical and experimental literature on predation of grouped prey (Parrish and Hamner 1997; Krause and Ruxton 2002), few scientists have studied preferences of 3-D predators attacking 2-D prey groups. There are many examples where this geometry might occur: white sharks (*Carcharodon carcharias*) attacking floating groups of seals

(Klimley 1994), diving birds attacking fish shoals at the water's surface, and fish attacking aggregations of spiny lobsters (*Scyllarides latus*) on the sea bottom (Lavalli and Spanier 2001). In these cases, predators typically have one hemisphere of maneuverability (which we call 3-D) and their prey is grouped at a substrate interface (e.g., ground-water, water-air, or ground-air). For this geometry, the selfish herd model may be inappropriate because if the predator comes approximately straight up or down on the group, there would not be a large proximity difference among targets and prey would therefore all have a similar "domain of danger" (Hamilton 1971; James et al. 2004; Quinn and Cresswell 2006). Domain of danger would now depend on the angle at which the predator attacked; the closer this angle was to perpendicular, the less the proximity argument holds. Therefore, the marginal predation prediction is called into question. One of the few other studies of a 3-D/2-D geometry is one in which individual sticklebacks (*Gasterosteus aculeatus*) attacked a rectangular strip of *Daphnia* (Milinski 1977a). That study supported the marginal predation hypothesis, and there were differences between the first and subsequent attacks. First attacks were typically directed at the highest prey density, whether peripheral, or central. However, overall attack preference was generally peripheral, especially if density was held constant (same nearest neighbor distance, NND) across the strip. Furthermore, predators were more selective (were more likely to attack the periphery) if they were relatively satiated. However, the generality of marginal predation when there is a 3-D/2-D geometry is difficult to evaluate based on this study alone because *Daphnia* are normally found in 3-D aggregations, which might influence the predator's innate attack behavior.

In this paper, we test whether the prediction that Hamilton and Vine made, which has been borne out in purely 2-D and purely 3-D predator/prey geometries, will hold up in a mixed (3-D on 2-D) predator/prey geometry. We do this by carrying out 3 manipulative experiments. In the first 2 experiments,

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largemouth bass (*Micropterus salmoides*) preys on freely moving whirligig beetle groups (*Dineutes discolor*) at the surface. In the third experiment, goldfish (*Carassius auratus*) preys on a fixed array of toad tadpoles (*Bufo bufo*) in which NND has been standardized and individual position choice within the group has been controlled for. By design, all 3 of the experiments prevented the occurrence of stragglers because stragglers are at an even greater risk than peripheral members of a group (Milinski 1977a, 1977b; Parrish 1989).

## METHODS

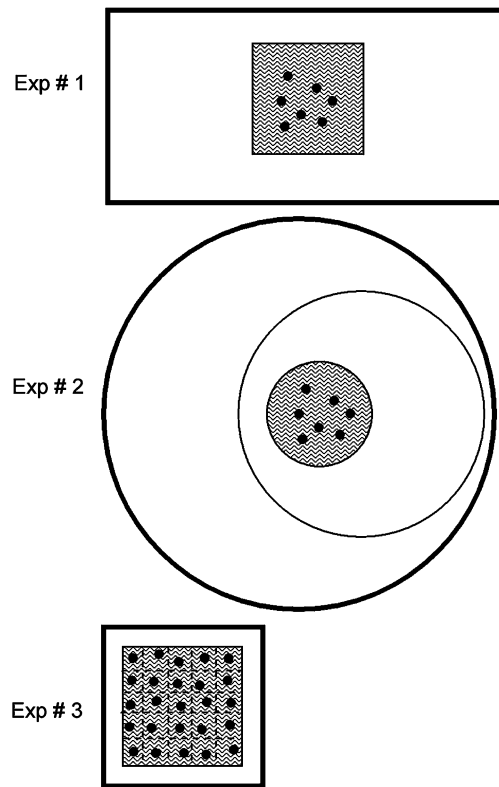
### Experiment 1

Ten largemouth bass (14–23 cm in length) were purchased from Ponderosa Farms in Afton, New York, and brought to the laboratory at the State University of New York at Potsdam where they were individually maintained on a 13:11 light:dark cycle in 38-l glass tanks (25 × 50 × 25 cm deep). Tanks were equipped with a 10-cm flowerpot for shelter and a Whisper power filter (model 20) and were surrounded by black plastic to minimize visual disturbance. Water was kept at room temperature (21 °C), and half was changed weekly. Bass were fed a satiation diet of ten 5 mm-sized floating pellets (Zeigler Silver Brand) per day for 2 weeks introduced remotely via small tubes into 15-cm diameter floating rings in the middle of the tank. Whirligig beetles were collected by dip net from the Racquette River, near Potsdam, New York; housed in stock tanks in the laboratory and fed ad libitum blood-worm fish meal for several days; and then returned unharmed to the river.

We recorded location of attacks using a remotely controlled Canon NTSC ZR20 Digital Video Camcorder. The camera was suspended on a mobile platform wheeled between fish tanks. Supplemental lighting was provided by a 75 W floodlight 2 m above. After a 2-week acclimation period for bass, food was withheld for 2 days before a trial. On the morning of a trial, activity level of each fish was assessed by putting one food pellet into each tank. Fish that did not eat were not used for that trial. Twenty beetles were then floated on fish tanks in a clear-bottomed plastic container (14 × 14 cm with 2.5 cm of water; Figure 1). The container kept whirligig beetles from dispersing and allowed fish to attack without consuming them and prevented stragglers. We filmed each fish for 2 min, removed whirligigs, and then fed fish their usual portion of food pellets. We filmed all active fish between 09:00 and 10:00 h on 3 separate days (“trials”) approximately 4 days apart using new beetles for each fish and trial.

From the digital video recordings, we obtained still images at the moment of each attack using Pinnacle Studio software (v.8). An attack was defined as a rapid lunge with mouth open and gills flared. The first 5 attacks were analyzed, although a few bass attacked less than this (see Results). From these still images, scaled  $xy$  coordinates of each beetle were obtained using Image-J software (Rasband 2004). Distance of each beetle to the geometric center of the group (Romey 1995) was determined (DTC) to the nearest millimeter. We then used Image-J to determine NND to the nearest millimeter at the time of the first and second attacks of the first 2 trials. For the attacked beetle in a group, its relative rank DTC and NND were determined (rankDTC and rankNND) as a percentage from the middle (DTC = 0 means that fish attacked the centermost beetle, whereas a DTC of 1 was the outermost beetle). We define a peripheral attack as one in which the attacked beetle had a rankDTC more than 0.5; that is, it was in the outer 50% of beetles.

The average attack preference of a fish was calculated by taking average rankDTC of 5 bites over 3 trials. A one-sample



**Figure 1**

Proportional top views of the 3 experimental test tanks. The inner shaded portion is where the prey group is held. In experiment 2, the container with the whirligigs is mounted on a large circular sheet of plexiglass to hold it asymmetrically in the tank, slightly away from the middle. Only a few of the prey have been shown in each diagram. In experiment 3, the prey are individually separated by partitions.

$t$ -test was used to test the hypothesis that the average rankDTC of attacked beetles was not 0.5. A repeated-measures analysis of variance (ANOVA) was calculated on the average rankDTC for each of 10 fish to determine if there was a difference in positions attacked between trials. These same procedures were also carried out for data on first attacks alone. To test for between-trial differences of NND and DTC, we took the mean of the whirligigs for the first photograph of each group on different trial days (a different group for each of the fish used) and used ANOVA. To determine if each beetle's NND and DTC were correlated, a general linear model regression was used while accounting for differences between trial days and groups; all the groups for the first attack of the first 2 weeks were used ( $N = 308$  beetles).

### Experiment 2

We conducted a further experiment on a subset of bass to determine whether tank size and asymmetry of the whirligig beetle group influenced attack preference. Five bass were kept individually in 100-l blue polypropylene circular tanks (25 cm diameter, 50 cm deep, Figure 1) filled with aged tap water. These tanks were twice as deep as those used in experiment 1 and gave the bass more maneuvering space. Water was maintained at 21 °C, as before, and one-third of the water was changed weekly. Whirligigs were floated over the bass in a circular container (15 cm diameter) constructed of a lucite cylinder affixed to an oversized plexiglass base (Figure 1). We fixed the lucite container asymmetrically on the base so that

the edge of the enclosure was in the middle of the fish tank, and we rotated the location of the inner circle in subsequent trials of a given fish. Beetles were given an acclimation period of 5 min so that they would group more tightly before reacting to the sight of the predator. A black tarp was placed between the fish tank and the floating whirligig container, and after 5 min it was pulled out slowly so the fish could see the whirligigs. Five fish were filmed individually in 3 separate trials (spaced by at least 4 days) for 10 min each. All fish were filmed between 10:00 and 12:00 h, and the first 5 attacks were analyzed. Analysis proceeded as in experiment 1. In addition, to test if the fish attack preference was confounded by the nearness of the group to the exterior tank, the location of the attack, relative to the fish tank wall, was noted where possible, specifically whether it was directed at the one-third of the whirligig group toward the wall or the one-third toward the middle. The number of bites directed toward these 2 sides was compared with a chi-square test.

### Experiment 3

In this experiment, we tested the attack preference of goldfish predators on toad tadpoles in which NND was fixed and prey distribution was randomized (to avoid biases due to correlation). The general methods used in this experiment are given elsewhere (Watt et al. 1997). Briefly, 5 goldfish in a  $20 \times 20 \times 25$  cm tank were presented with a fixed array of 25 toad tadpoles in a floating arena made up of a  $5 \times 5$  matrix of 20-ml tubes ( $15.5 \times 15.5$  cm) (Figure 1). The arena floated on the surface. Matt black paper surrounded the tank to reduce disturbance. The tank was elevated, and attacks were observed via a mirror placed under the tank. NND of each tadpole was held constant. In this experiment, predators were used in a group rather than individually as used in experiments 1 and 2 and were not independent. Position of each attack was recorded visually for 10 min per day for 14 days. Tadpoles were returned to a stock tank after each trial, and a new batch of tadpoles was selected. We defined peripheral attacks as those occurring toward the outermost 16 tadpoles and central attacks toward the innermost 9. For the total attacks in 10 min, mean percentage of peripheral attacks was calculated for each of 14 trials, and a Wilcoxon signed-rank test was used to determine if the ratios were not equal to 64% (16 peripheral positions of a total of 25). For analysis of the position of the 14 first attacks in a trial, a chi-square test was used.

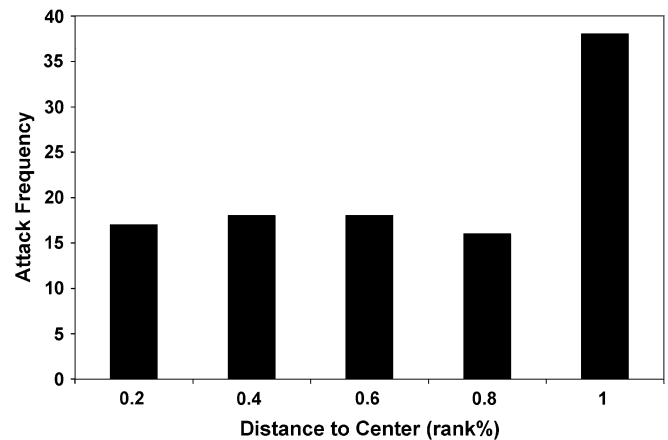
## RESULTS

### Experiment 1

RankDTC of attacked beetles was significantly greater than 0.5 (one-sample *t*-test,  $t = 3.161$ , degrees of freedom [df] = 9,  $P = 0.012$ , mean = 0.634); on average, bass attacked peripheral beetles more (Figure 2). There was a significant difference in mean rankDTC between trials; fish were more likely to attack peripheral beetles in later trials than in earlier ones (repeated-measures ANOVA:  $F_{2,10} = 5.23$ ,  $P = 0.028$ ), and there was a significant linear trend in rankDTC over the 3 trials ( $F_{1,5} = 17.48$ ,  $P = 0.009$ ). On average, 8.3 of the 10 fish attacked per trial, and each fish attacked the prey group 4.3 times during the filming period.

When analyzed separately, bass's first attacks were not significantly targeted at peripheral whirligigs (one-sample *t*-test:  $t = 1.13$ , df = 9,  $P = 0.284$ , mean = 0.583). Nor was there a significant difference between trials of rankDTC of first attacks (repeated-measures ANOVA:  $F_{2,10} = 0.652$ ,  $P = 0.541$ ).

Mean per-group NND and DTC of whirligig groups were not significantly different between trial days (ANOVA for



**Figure 2**

Experiment 1: frequency histogram of total number of fish attacks ( $N = 107$  bites) relative to the rank distance of each whirligig to the center of the group. X-axis labels represent the upper end of each range (e.g., 0.8 = attacked beetle was in the 60–79 percentile away from geometric center).

DTC among 3 trial days:  $F_{2,22} = 0.466$ ,  $P = 0.645$ ; for NND between first 2 trial days:  $F_{1,16} = 0.014$ ,  $P = 0.904$ ). Peripheral beetles had a larger NND than central ones (ANOVA with attack and trial as dummy variables:  $F_{11,306} = 2.268$ ,  $P = 0.0014$ ). However, fish were not more likely to choose prey with larger NND; for first attacks in trial 1, rankNND was higher than 0.5 in 4 of 7 fish and in trial 2, 6 of 10 fish.

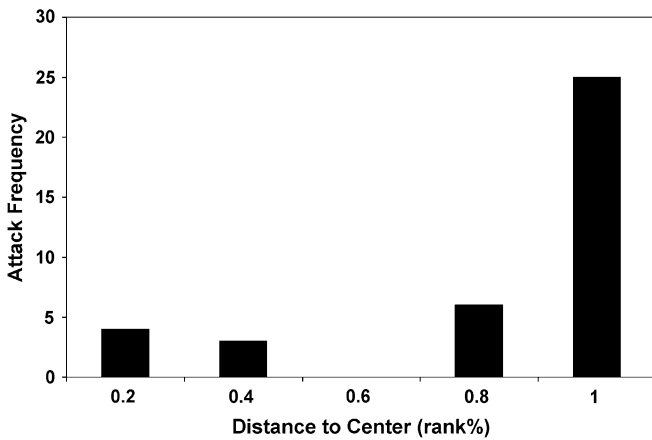
### Experiment 2

Fish attacked beetles whose mean rankDTC was significantly greater than 0.5 (one-sample *t*-test:  $t = 5.73$ , df = 4,  $P = 0.005$ , mean = 0.684, Figure 3). There was no significant difference in rankDTC between trial days (repeated-measures ANOVA:  $F_{2,4} = 1.07$ ,  $P = 0.422$ ). Mean number of fish that attacked per trial was 4.0, and mean number of attacks per fish was 3.2.

In contrast to experiment 1, first attacks were significantly targeted at peripheral whirligigs (one-sample *t*-test:  $t = 3.8$ , df = 4,  $P = 0.019$ , mean = 0.806). There was no significant trial effect of rankDTC for first attacks (repeated-measures ANOVA:  $F_{2,4} = 0.459$ ,  $P = 0.66$ ). Whirligig beetles grouped more tightly and were less active in experiment 2 than experiment 1 because of the added acclimation procedures. The tank wall did not appear to influence the attack preferences of fish; there was a nearly equal probability that fish attacked toward (11 cases) versus away (10) from the closest wall of the fish tank (chi-square test:  $P > 0.05$ ).

### Experiment 3

As in the 2 previous experiments, the goldfish predators attacked peripheral tadpole prey significantly more often (Figure 4). Results were similar to experiment 1: average attacks were more likely to be peripheral, but first attacks were not. Specifically, when considering all attacks ( $N = 203$  attacks, mean attacks per trial = 14.5), the mean of trial means of peripheral to central attacks was 0.747, significantly greater than the expected mean of 0.640 (one-sample Wilcoxon signed-rank test:  $N = 14$ ,  $P = 0.028$ ). However, when considering first attacks, goldfish were no more likely to attack peripheral versus central prey (in 9 of 14 cases, fish attacked peripheral prey [chi-square test,  $P > 0.05$ ]). Attacks were widely distributed among tadpoles; there was no observed preference for one tadpole over another. Also, there was no

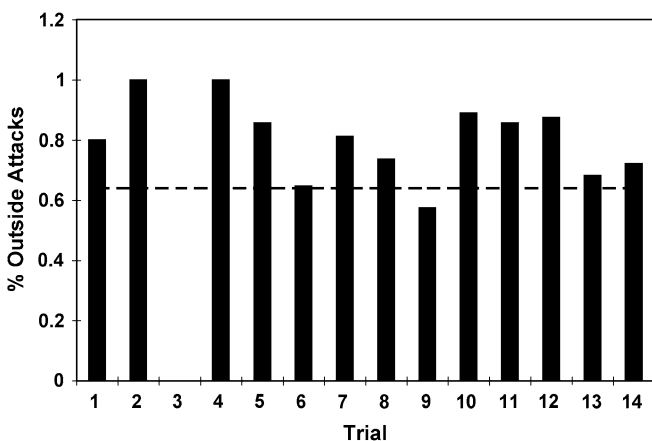


**Figure 3**  
Experiment 2: frequency histogram of total number of fish attacks ( $N = 38$  bites) relative to the rank distance of each whirligig to the center of the group. X-axis labels represent the upper end of each range (“0.8” = attacked beetle was in the 60–79 percentile away from geometric center).

significant increase in the percentage of peripheral attacks over time ( $F_{1,12} = 0.08$ ,  $P = 0.779$ , Figure 4).

**DISCUSSION**

The marginal predation prediction was supported in all 3 experiments, regardless of species, density of prey, and predator-maneuvering space. This is strong support for marginal predation under 3-D/2-D geometry. In experiment 1, bass did not show an initial attack preference based on position, but the average of 5 bites was significantly peripheral. This is similar to Milinski’s findings (Milinski 1977a), although he found a significant preference for the densely populated middle positions for first attacks before they moved to the margin. Although whirligigs were significantly more dense in the center than periphery (smaller NND), there may not have been a big enough difference for the fish to respond. Unconstrained whirligig groups also exhibit a reduced NND at the center (Romey 1995).



**Figure 4**  
Experiment 3: the proportion of attacks directed at the outside cells of the fixed prey group for 14 trials. The dashed line represents the expected proportion if there was no attack preference by the goldfish. In 12 of 14 trials, there were more attacks on peripheral prey than expected. In trial 3, there were no attacks to peripheral tadpoles.

The increased selectivity of bass for the periphery on successive trial days may have several causes such as learning or a change in satiation. Prior to the experiments, bass had not experienced whirligigs and may have obtained feedback on the first several trials that allowed them to refine their attack behavior or they may have become acclimatized to the experimental apparatus. Satiation has been shown to influence selectivity of predators attacking groups. For example, Milinski (1977a) showed that satiated sticklebacks are more selective than hungry ones. In our experiment, although predators received the same total ration of food every day, there may have been a cumulative effect on satiation over the experimental period. Observed differences between trials do not appear to be due to differences in the beetle’s behavior; their mean NND and DTC did not differ significantly between trials.

In experiment 2, fish tanks were twice as deep as those used in experiment 1 and bass generally remained at the bottom except to feed. The fish came up from more directly below whirligig groups than in experiment 1, yet the results were nearly the same (mean rankDTC = 0.634 in experiment 1 and 0.684 in experiment 2). In contrast with experiment 1 though, the first attacks were significantly directed toward the periphery, and there was no significant difference between trials. This suggests that the proposed pattern of learning and satiation seen in experiment 1 was even better developed in experiment 2, 2 months later. The increased level of marginal predation observed in experiment 2, despite the reduced sample size of fish, may also be related to increased density of whirligigs. They group more tightly in autumn (Hatch 1925), and the added acclimation period (5 min while shielded from sight of the predator) allowed the beetles to stabilize their positions. This similar result despite differences in methodology strengthens our findings that marginal predation occurs under a variety of circumstances.

In experiment 3, first attacks were not peripheral, but average attacks were. Experiment 3 adds robustness to our main finding because it represents a different size ratio between predator and prey. Also, even though goldfish were foraging in groups of 5, marginal predation still occurred. This differs from the findings of other researchers who have found that when predators are in groups working together, they sometimes attack the center of prey groups (e.g., in cetaceans [Norris and Schilt 1988]). However, there is little evidence that goldfish forage cooperatively (Pitcher et al. 1982).

Our general result, that marginal predation occurs when a predator has equal access to all members of a prey group, has implications on theories of how predator preference shape the evolution of grouping in prey. Many authors have assumed that proximity is a primary reason that predators attack peripherally (e.g., Hamilton 1971; Vine 1971; Bumann et al. 1997). However, our results show that marginal predation occurs even when the proximity issue is reduced. In experiment 2, the fish came up from even more directly below than in experiment 1 but both chose marginal prey at a similarly high rate. Future studies that directly manipulate this attack angle would be enlightening. Our findings are also important in understanding grouping trade-offs; they confirm previous assumptions that peripheral whirligigs make a trade-off between more food (Romey 1995) and higher predator risk. In addition, if marginal predation is widespread among predators, then it makes the evolution of grouping as a response to multiple species of predators stronger (Sih et al. 1998).

Given our results, proximity alone does not explain why predators selectively attack peripheral individuals, casting doubt on the selfish herd hypothesis. Alternative explanations for marginal predation, such as the confusion or correlation hypothesis, need to be examined more carefully in future

studies. The confusion effect (Landeau and Terborgh 1986) rests on the assumption that there is a limit to a predator's ability to track multiple targets, that there is a bottleneck in neural pathways of the optic system, as simulated by 2 recent studies (Krakauer 1995; Tosh et al. 2006). The confusion effect also predicts that it would be easier for predators to attack peripheral prey because there would be fewer individuals in the predator's visual field and that the predator could potentially separate out one individual it could focus on. An experiment in which prey group size was varied and the response time of predators was measured would be illuminating. The correlation hypothesis (as reviewed by Stankowich 2003) suggests that predators attack the margins of prey groups not because of an individual's position but because its position is correlated to some state variable such as age or size of prey. This has been documented in static groups of spiders (Rayor and Uetz 1993). Studies such as our experiment 3 and that of Milinski (1977a) attempt to control for this by randomly placing prey into fixed wells. This allows us to conclude that predators are not actively choosing individuals because of observed differences during the experiment. However, predators might have an innate preference for edges because peripheral individuals in the past have typically been younger or less well defended. More studies on the correlation between position and state variables of prey groups would help to understand whether these correlations exist and act as a possible explanation for marginal predation. In whirligig beetles, there is a correlation of position with hunger (Romey 1995) and sex (Romey and Wallace 2007) but not for body condition (Romey, submitted) or defensive chemicals (Romey and Wallace 2007). Finally, in amphibians, metamorphic stage (and therefore mobility) could influence position (Arnold and Wassersug 1978).

In the present study, we used a variety of species and experimental methods to explore the existence and pervasiveness of marginal predation. Unlike other studies of matched dimensions (e.g., 2-D on 2-D), we did not find that predators always choose prey with the largest NND. In experiment 2, even though there was a correlation between DTC and NND, bass did not significantly target beetles with the larger NND. However, in one study of 3-D/2-D geometry, Quinn and Cresswell (2006) found that sparrow hawks (*Accipiter nisus*) preferentially attack redshanks (*Tringa totanus*) that have a larger NND. It would be beneficial to do more simulation work to see if neural network models (Tosh et al. 2006) support the prediction that edge individuals are less confusing than center individuals because of their position, rather than just their NND.

Our results demonstrate marginal predation under 3-D/2-D geometry. This helps us to understand the evolution of grouping in general and raises new questions about the mechanisms leading to marginal predation. The existence of marginal predation in other swimming or flying predators that attack prey groups at substrate interfaces remains to be tested.

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