Computerized stimuli for studying oddity effects

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Abstract

Visually hunting predators must overcome the challenges that prey groups present. One such challenge is the confusion effect where an overburdened visual system means predators are unable to successfully target prey. A strategy to overcome confusion is the targeting of distinct, or odd, individuals (the oddity effect). In live prey experiments, manipulation of group member phenotypes can be challenging and prey may differ on more than the single feature one intends to define as odd. The use of highly controllable computerized stimuli to study predator-prey interactions is increasingly popular in the field of behavioral ecology. However, to our knowledge, the validity of computerized stimuli to study the oddity effect has not been established.

Predator choice experiments were conducted using naive stickleback predators to ascertain whether the oddity effect could be demonstrated in the absence of live prey.

We found evidence for both the oddity effect and preferential targeting of group edges and low density regions, as would be predicted if predators targeted prey individuals to minimize confusion. The oddity effect was evident at a low threshold, above which dots were no longer perceived as odd, and no longer attacked more often than expected by chance.

We conclude that computerized stimuli are an improved, practical method for studying oddity effects while further validating the use of similar methods for studying other aspects of visual predation. In addition to higher control of ‘prey’ appearance, the replacement of live prey animals with digital stimuli is ethically beneficial and reusing code improves experimental efficiency.

Keywords: oddity effect, confusion effect, visual predation, predator, prey, marginal predation, computerized prey

Data accessibility

Analyses reported in this article can be reproduced using the data located at DOI:10.5061/dryad.dq0tt96

Introduction

When predators approach a group of prey they are simultaneously presented with a choice of potential targets. Which prey within a group are selected by predators directly affects the composition of phenotypes within a group, in addition to driving the evolution of prey grouping behaviors (Croft et al., 2009; Rodgers et al., 2015). Visually hunting predators may select prey because of their position in the group (Hamilton, 1971), or because of their appearance (Ohguchi, 1978). Prey may be preferentially targeted because they appear slow or weak (Genovart et al., 2010), because they are the appropriate size to maximize energy gains (Turner, 1982), or because they are visually distinct from the rest of their group (the oddity effect, Almany et al., 2007; Penry-Williams et al., 2018).

Landeau and Terborgh (1986) used bass preying on groups of minnow to demonstrate that the presence of visually distinct ‘odd’ prey mitigates the confusion effect. The confusion effect describes the diminished ability of a predator to successfully target an individual within a group, resulting from cognitive limitations (Krakauer, 1995). Landeau and Terborgh (1986) is a well-cited oddity effect study, showing how individual appearance and overall group composition can affect predation decisions and outcome. However, a methodology that uses live, vertebrate prey, which are confined with the purpose of being attacked, is something we are less likely to deem ethically acceptable by today’s standards (Buchanan et al., 2012; Brown, 2015; Sloman et al., 2019). A more common predator-prey system for studying confusion and oddity effects is that of stickleback (*Gasterosteus aculeatus*) preying on *Daphnia*. Putting aside any philosophical questions about ethics and (the lack of) vertebrae (although see Freelance, 2018), there are potential issues relating to efficiency and perception that may arise here.

In order to understand how phenotype contributes to the oddity effect, prey group members should ideally only differ on a single feature. Many studies examining predator selection of odd prey require prey individuals to be sorted by size and dyed, usually with food coloring (Landeau and Terborgh, 1986; Wilson et al., 1990; Richards et al., 2011; Rodgers et al., 2013; Penry-Williams et al., 2018). This process is time consuming and largely reliant on a human judgment of prey similarity. Perception is highly subjective, even between members of the same species (Brainard and Hurlbert, 2015) and consequently this raises potential issues for repeatability. In addition, studies of confusion and oddity effects use the human visual system to establish uniformity of prey appearance, yet stickleback, for example, are able to see ultraviolet (UV) light (Modarressie and Bakker, 2007; Rick et al., 2012). Hence, what might appear to be a largely homogenous stimulus group in visible light might not be the case elsewhere in the electromagnetic spectrum. Although there are ways to overcome between-species perceptual differences (e.g., Rowe et al, 2006), we submit below that rendering digital stimuli monochromatically and through a UV-filter affords the highest standard of stimulus control.

An alternative to altering prey appearance is to use color-morphs of the same species. In the case of *Daphnia*, morphs can be obtained through manipulating water chemistry (Ohguchi, 1978). However, different behavioral phenotypes often present themselves alongside differences in appearance. For example, higher levels of aggression are seen in melanic vs. silver mosquito fish (*Gambusia holbrooki*, Horth, 2003) and blue vs. yellow cichlids (*Astatotilapia burtoni*, Dijkstra et al., 2017). Black springbok (*Antidorcas marsupialis*) have lower activity levels than their white or standard colored counterparts (Hetem et al., 2009), and while both black and white mollies (*Poecilia latipinna*) shoal with color-matched conspecifics, white morphs have a stronger overall shoaling tendency (Rodgers et al. 2013).

Uncontrolled differences in behavioral phenotype have the potential to confound studies that are aiming to isolate a feature that may influence predator choice.

As we suggest above, a possible solution to improve experimental efficiency and to better control prey phenotype is to use computerized stimuli in place of live prey. Individuals within simulated ‘prey’ groups can be manipulated to differ from their group-mates only in the specific, measurable ways intended by the experimenter. The use of computerized stimuli to study visual search and attentional capture is well established in experimental psychology (Bundesen and Habekost, 2008). There is also considerable research in the field of behavioral ecology examining the confusion effect, with human predators preying on computerized targets (Ruxton et al., 2007; Scott-Samuel et al., 2015; Hogan et al., 2017a; Hogan et al., 2017b). Computerized stimuli are also gaining popularity for studying some aspects of visual predation in non-humans (Ioannou et al., 2012; Woo et al., 2016; Duffield and Ioannou, 2017; Ioannou et al., 2019). However, to our knowledge, the effectiveness of similar methods for studying oddity is yet to be validated for non-human predators.

Here, we use stickleback targeting computerized prey-dots to establish the value of this approach to the study of the oddity effect, defined here as the preferential targeting of a minority phenotype (Ohguchi, 1978; Penry-Williams et al., 2018; Raveh et al., 2019). If the use of digital stimuli is a valid methodology for exploring oddity effects, we would expect to see that a minority phenotype becomes preferentially targeted below a certain threshold of representation within the group. For applicability to the general study of visual predation, predators should target computerized prey groups as they do live prey groups. Thus, we would expect, in line with work on live prey, to also see preferential predation of those on the edges of groups (Hirsch and Morrell, 2011).

Methods

Stickleback sourcing and maintenance

Three-spined stickleback (n=56) were sourced from Thwaite Hall Gardens, Cottingham, UK (grid reference: TA 055 326) in October, 2015. A further 200, wild caught stickleback were sourced from The Carp Co. (Bourne Valley Fish Farm, Kent, UK) in September, 2016. Fish from the Thwaite Hall Gardens source were caught using telescopic landing nets and transported back to the laboratory, by car, in a 20L bucket filled with pond water. No fish died in transit or immediately after being transferred to the laboratory tanks.

All fish were quarantined for 3 weeks in two 150L tanks, aerated with two Tetra APS 50 air pumps and two 30 mm air stones per tank. Manual water changes of 25-50% were made 2-3 times per week. After this period, fish were housed in groups of 12 on a closed, freshwater system with ~20% new water introduced per week. Fish were fed daily on defrosted frozen bloodworms and *Daphnia* spp. (Ings Lane Garden Centre, Hull, UK). Water temperature was kept between 10-12°C and the day:night light cycle was set at 12:12 h to prevent the onset of breeding condition. As a result, no attempt was made to determine the sex of individual fish. Experimentation took place between 09:00 and 18:30 h, as stickleback are diurnal, visual predators (Wootton, 1976; FitzGerald and Wootton, 1986).

Experimental tank setup

Experiments took place in a modified glass aquarium (figure 1). The aquarium was split into a companion area spanning the full width of the tank at one end (10 cm x 20 cm, figure 1a) and a larger focal area (20 cm x 20 cm, figure 1b). The companion area contained 3 non-experimental fish. The companion fish acted to reduce stress to the test fish by providing a social environment for this shoaling species (Jones and Godin, 2009; Voellmy et al., 2014). A transparent, perforated partition allowed visual and olfactory contact between the companion fish (in the companion area) and the focal fish (in the focal area). The walls of the companion area were covered with black, opaque plastic to minimize brightness, and therefore stress (Maximino et al., 2010), to the companion fish. An opaque lid covered the companion area so companion fish were not disturbed when focal fish were netted in and out of the experimental tank. The focal area of the tank was partially divided by a black, opaque barrier. This provided a shaded refuge area for the test fish, from which the projection (see below) was not visible. A plastic plant within the experimental area provided further refuge for the test fish.

Simulated prey (see below for details of the simulation) were rear-projected onto a self-adhesive, rear projection film (model: GR/Gray, brand: ARCHISTAR) adhered to the tank wall (figure 1b). A Sony VPL-DX122 LCD projector connected to a Toshiba Portégé Z30-B-10G Ultrabook was used to project the simulated prey. The progressive scanning of the 60Hz LCD screen and the constant lamp output of the projector ensured that the critical flicker frequency of stickleback, thought to be higher than humans (Healy et al., 2013), is unlikely to be an issue here (for full explanation see Künzler and Bakker, 2001, pp 681-682).

To reduce brightness and glare, the projector was placed behind a screen (Solar Control High Reflective Silver Window Film, The Window Film Company UK Ltd, Chesham, UK). The screen also functioned to reduce heat and UV transmission by 77% and 99% respectively. Two webcams (Microsoft LifeCam Cinema), connected to a second laptop (Samsung NP-

R780-JT3BUK) were placed outside of the tank, facing the projection wall, to allow for data collection (see Experimental Procedure, below). Webcam 1 (figure 1) was positioned above the waterline and allowed observation of the fish exploring the tank and approaching the projection. Webcam 2 was placed directly below webcam 1 and allowed underwater observation of the fish attacking the simulated prey group.

Simulation of prey

All simulations were carried out using OpenSesame v3.0.7 (Mathôt et al., 2012), using a screen resolution (canvas) of 1360 x 768 pixels. The canvas was colored an intermediate shade of grey, RGB(129,129,129). N_{group} dots ($N_{group} = 16$) were positioned on the canvas by selecting pseudorandom integer values from a uniform distribution between x_{min} and x_{max}, and between y_{min} and y_{max} for each dot i (see supplementary table 1 for details of parameters used in the simulation). The minimum and maximum values of x and y were chosen to define an active area of the canvas suitable for projection onto the experimental tank, and gave an approximate projected array area of 3 x 7 cm. Each dot had a radius r of 7.5 pixels, centered on (x_i, y_i), and a pseudorandom orientation (movement direction, d_i) between 0 and 2π radians. Dots were colored (c_i) according to whether they were odd or a distractor (the remainder of the group). Dots $1 \leq i \leq N_{odd}$ were colored as specified by shade of the odd dot, and the remainder the shade of the distractors (see table 1 for number of odd dots). 'Dark' dots were defined as RGB(1,1,1) and 'light' dots as RGB(255,255,255). Dots therefore differed from one another in luminance, but not color. The combination of achromatic stimuli presented through a UV-filter ensured that prey stimuli could not be differentiated on the basis of hues that are invisible to humans (Oliveira et al., 2000; Baldauf et al., 2008). A circular dot shape was chosen to represent the prey. This avoided the assumption that other projected shapes, such as those of natural prey, would be viewed as such by the stickleback.

In each timestep t, the position of each dot was updated such that:

$$x_{i(t+1)} = x_{i(t)} + v * \cos(d_i)$$

$$y_{i(t+1)} = y_{i(t)} + v * \sin(d_i)$$

The value of v ($v = 1.5$) was selected such that the dots appeared to move smoothly and continuously to a human observer. To ensure that the dots did not move in straight lines, after the position of dots had been altered, their orientation was adjusted such that:

$d_{i(t+1)} = d_{i(t)} + a_{max} * (b_i - 0.5)$, where b is a pseudorandom number between 0 and 1.

Random motion is common in many zooplankton species (Seuront et al., 2003; Komin et al., 2004; Strickler et al., 2005) and the random elements of swimming behavior will elicit attack from predatory fish (Matsunaga and Watanabe, 2012).

For any dots that left the canvas (where any of $x_i > x_{max}$, $x_i < x_{min}$, $y_i > y_{max}$ or $y_i < y_{min}$), orientation was updated such that $d_{i(t+1)} = d_{i(t)} + \pi$, meaning that they reversed direction and 'bounced' back into the group. This ensured that the group did not become more dispersed during the simulation, mimicking natural groups where compaction is maintained (Seghers, 1974; Magurran and Pitcher, 1987). The simulated dots will henceforth be referred to as 'prey-dots'.

Experimental procedure

The experimental tank (figure 1) was filled to a depth of 13 cm of system water, with an olfactory cue added to stimulate predatory feeding behavior (Johannesen et al., 2012). The olfactory cue was made by defrosting 2 blocks of Gamma brand frozen *Daphnia* in 20ml system water. The *Daphnia* were then strained through a fine mesh net to ensure that the cue contained no solids. Three non-experimental fish were carefully netted into the companion area (figure 1a) 5-10 min before experimentation commenced. Companion fish had visual and olfactory contact with the focal fish in both the refuge area (figure 1a) and experimental area (figure 1b), but their view into the experimental area was partially obstructed by a plastic plant. Companion fish were not used as test fish.

At the start of each trial, the focal fish was netted from the holding tank into the refuge area, and the prey simulation was started. Within a single trial a fish was presented with up to 7 arrays (prey-dot groups). Fish were allowed 20 min to attack the first group of prey-dots within a trial. For each subsequent prey group, fish were allowed up to 10 min to attack. The additional 10 min of time to attack the first group was to allow for acclimatization and tank exploration. If an individual continued to show interest in the stimuli, by attacking prey-dots within the allotted time, it was presented with up to 7 treatments out of a possible 11 (table 1). In a first set of trials (N=35 fish) prey-dot groups were homogenous (0-odd, 16 dark or 16 light prey-dots), equal (8-odd), 2-odd and 4-odd (table 1). In a second set of trials (N=34 fish) prey-dot groups were homogenous, equal, 1-odd and 3-odd (table 1). Groups in both sets were presented in a random order.

Each individual trial ended either when the fish made an attack towards a prey-dot, or when the allotted attack time expired. As the fish attacked, the experimenter froze the moving prey-dots by pressing the spacebar, then used the mouse to click at the position of the attack. The coordinates and phenotype of each prey-dot, in addition to the coordinates of the mouse click, were recorded for use in analysis. If the experimenter froze the array > 0.45 sec before or after the fish made contact with the screen this was noted as a failed trial and the experimenter moved on to the next prey-dot group. 0.45 sec was equivalent to a timescale where the dots had visually (to a human observer) shifted position. This occurred on 93 out of 339 occasions in total. The proportion of these occurrences were similar across each treatment type, with no significant difference between the greatest number of occurrences (9/27 trials in the 4 light:12 dark array) and the fewest (4/27 trials in the 3 dark:13 light array; proportion test: x = 1.621, p = 0.203).

At the end of the trial, fish were measured to the nearest 0.1 mm (standard length) using dial calipers before being put back in their system tank. A total of 87 fish were tested, however 18 fish did not make a first attack within 20 min and 2 fish were removed from analysis due to experimenter error, resulting in a final sample size of n=67, (standard length 28.4-51.7 mm), see table 1 for breakdown of sample sizes by treatment. A total of 197 attacks were made, with a mean of 2.95 attacks per fish.

Data Analysis

Data were analyzed in R v.3.3.1 (R Development Core Team, 2015). A binomial test was used to assess whether the proportion of attacks made towards light and dark targets differed from random expectation in the equal ratios treatment. As there was no significant deviation from random (13 attacks to dark, 21 attacks to light; binomial test, p = 0.230), fish could be said to express no particular preference for light or dark dots, so data were pooled by the number of odd individuals for all further analysis.

We used generalized linear mixed effects models (package lme4 1.1–12; Bates et al. 2015) to explore the effects of oddity status (odd or not), number of odd individuals (treatment), position (center or edge of the group) and local density (distance to the nearest neighbor), and their interactions on whether or not a dot was targeted (target = 1, not target = 0). Trial number nested within fish ID was added as a random effect (random intercepts) to account for the repeated measures nature of the data (multiple dots per trial and multiple trials per fish). An observation-level random effect (random intercepts) was also added to account for over dispersion in the data (Harrison, 2014). There was no collinearity between the main effects (VIF≤2.5). Body length and the site from which fish were sourced were initially checked and found to have no effect on target choice (supplementary table 2). Both were left out of further analysis to focus on variables of interest.

We identified a set of candidate models, including all possible combinations of pairwise interactions between the four variables, plus the model including all three-way (and lower order) interactions and the model containing the 4-way interaction (and all lower order interactions). Every model contained the 4 main effects. This gave a total of 66 candidate models. We ranked these models by AIC_C scores and assigned them Akaike weights (ω_m) based on these scores (package MuMIn 1.40.0, Barton, 2017). All models with AIC_C within 2 of the best model AIC_C ($\Delta AIC_C \leq 2$) were included in the top model set. We calculated full averaged estimates for each variable and interaction appearing in the top model set (i.e. model-weighted averages of predictor estimates over all top set models including those that did not contain the predictor). We also calculated the relative importance of explanatory variables (ω_p; the sum of Akaike weights of all top set models containing the variable). We reanalyzed our data using the mean distances to the 2-4 closest neighbors in place of the distance to the nearest neighbor and found the results to be broadly consistent (supplementary table 3).

Further binomial tests were used to assess whether fish attacked odd individuals more often than expected by chance given their frequency in the group, and a proportion test was used to assess whether edge individuals were attacked more often than expected by chance, given the likelihood of an individual being defined as ‘edge’.

Ethical statement

Experiments were approved by the University of Hull's School of Biological, Biomedical and Environmental Sciences and Faculty of Science and Engineering ethical review committees before commencement (reference numbers U094 and U095), and followed the Association for the Study of Animal Behaviour Society Guidelines for the treatment of animals in behavioral research and teaching (ASAB/ABS, 2018). Care was taken to minimize stress to the experimental fish by the provision of companion fish and refuge areas during the experiment, and by careful handling.

Results

All models in the top model set (table 2) contained an interaction between oddity status and the number of odd individuals in the array on the likelihood of a particular dot being attacked (table 3). Odd individuals were more likely to be attacked, but only when there were 1 or 2 (rather than 3 or 4) in the array (binomial tests: table 4; figure 2a). The models also highlighted that edge individuals (table 3; proportion test: X^2=63.874, df=1, p<0.001; figure 2b) were attacked more often than those in the center of the group. These results were broadly robust to the choice of nearest neighbor distance as a measure of local density (supplementary table 3), however, including 3 or 4 neighbors (but not 2) in the measure of local density showed that those with higher average nearest neighbor distances (low local density, or more isolated individuals) were more likely to be attacked (supplementary table 3b and c; figure 2c).

Discussion

Using luminance oddity, we have validated the use of computerized stimuli to study the oddity effect. We were able to demonstrate preferential targeting of a minority phenotype, in line with the oddity effect (Ohguchi, 1978; Penry-Williams et al., 2018). 2D arrays were attacked as you would expect if they were 3D, confusing prey group, with preferential targeting of the edges and low density regions (e.g. Hirsch and Morrell, 2011; Duffield and Ioannou, 2017). Other studies have used virtual stimuli to successfully examine the confusion effect (Scott-Samuel et al., 2015; Hogan et al., 2017b), marginal predation (Duffield and Ioannou, 2017), the coordination of prey movement (Ioannou et al., 2012; Lemasson et al., 2016) and the targeting success of humans predating odd prey (Ruxton et al., 2007). However, to our knowledge, this is the first demonstration of the oddity effect using a naïve, non-human predator preying on computerized prey.

The predatory response of fish to the 2D prey group adds to the work validating the use of virtual prey for studying visually mediated predation (Ioannou et al., 2012; Woo et al., 2016;

Duffield and Ioannou, 2017; Ioannou et al., 2019). We found that individuals on the periphery of the group were significantly more likely to be targeted than those in the center. This aligns with what would be expected of a pursuit predator attacking a prey group (Hirsch and Morrell, 2011), and with studies examining marginal predation in relation to confusion effects (Duffield and Ioannou, 2017). Targets were significantly more likely to be further away from their nearest neighbors, i.e. they had lower local density, or were more isolated within the group. These findings are contrary to the idea that denser regions of a group attract attention due to higher conspicuousness (Ioannou et al., 2009), but in line with findings that show increased risk to prey at lower local densities (Ioannou et al., 2009; Ioannou et al., 2019).

Detection and selection occur at different stages of the predation process. Fish may be initially drawn to denser regions of the group at the detection stage but choose to target less dense (and less confusing) regions at the attack stage (Milinski, 1977). While we did not measure success, evidence suggests that attacks are more successful when local prey density is lower (stickleback preying on *Daphnia*; Ioannou et al., 2009) or prey individuals are isolated from the group (geckos *Eublepharis macularius* and marmosets *Callithrix jacchus* preying on mealworms, Schradin, 2000). Consequently, a targeting preference for less dense regions can be considered a strategy for overcoming the confusion effect.

Attacking dense regions is more perceptually challenging and therefore takes more focus, at the expense of awareness of surroundings. Stickleback are less likely to notice a predator when attacking a dense swarm, and when they are exposed to a predator before being presented with a prey group, they will target areas of lower local density (Milinski, 1984). Bees have increased difficulty finding a target flower within a group of higher density distractor flowers (Spaethe et al., 2006). In humans, increased density, or visual clutter, contributes to crowding effects, impairing the identification of targets (Whitney and Levi, 2011), although this phenomenon can be overcome if targets are salient because they are visually distinct i.e. they are odd (Põder, 2002).

Odd prey-dots were significantly more likely to be targeted when groups contained 1 or 2 odd prey-dots, but not when there were 3 or 4. These results suggest that joining a majority unmatched group may not necessarily increase predation risk for minority phenotype individuals, above a low threshold. However, we cannot say whether this threshold is an absolute number or proportion as we only tested a single group size of 16 individuals. Landeau and Terborgh (1986) found that when 1 or 2 odd colored minnow, but not 4, were present within a prey group of 8, bass were significantly more likely to make a successful attack to any group member, odd or otherwise. This effect did not scale up to group sizes of 15, where no 5 minute trials ended in a successful attack, and thus the question of absolute or proportional thresholds could not be answered. In longer experimental trials, lasting 24 hours, Theodorakis (1989) demonstrated bass preferentially targeting size-odd minnow below a threshold of 5, but again this was only in a single group size of 30.

Fish are commonly used to study the oddity effect, however a diverse array of animal species respond to digitally generated stimuli (e.g. blue jays *Cyanocitta cristata*, Bond and Kamil, 2002; baboons *Papio papio*, Fagot et al., 2009; chameleons *Chamaeleo chamaeleo*n, Katz et al., 2015; jacky dragon *Amphibolurus muricatus*, Woo et al., 2016) and therefore computerized stimuli to study oddity, and other aspects of visual predation are applicable across species. Computerized stimuli form the foundation of studies of attentional capture in experimental psychology (Bundesen and Habekost, 2008) but little is known about attentional capture in other species, particularly fish. Adaptations of the present methodology could be used to address the dearth of research in this area.

Computerized stimuli appear to be a viable and practical method for studying oddity effects, but there is still much to learn about when and why oddity effects occur. While we have demonstrated a preference for odd targets at a low threshold within a group, we cannot make conclusions about what drives the preference we have observed here. The targeting of odd prey may have resulted from attentional capture by odd targets, or because targeting odd prey reduces confusion effects. Further work, using a similar methodology to that presented here, could be used to establish the threshold of 'useful' oddity, i.e. oddity that improves attack success, and how this interacts with prey group size. In addition, while we found no evidence that oddity interacted with the preference for edge and low density regions,

We propose that the use of computerized 'prey' is an improved method for studying oddity effects, for the following reasons:

1. Digital stimuli are highly controllable and reduce the potential for confounding factors.
2. Ethical practice is improved because the number of live prey required for experiments are reduced.
3. Once written, code can be shared and reused, greatly improving experimental efficiency and output.

Table 1 The 11 possible prey-dot group compositions, including the number of experimental trials (*N* experiments) per treatment.

Group type	***N* experiments**	**N_{odd}**	**dark : light**	**Set**
1-odd	16	1	1:15	2
1-odd	15	1	15:1	2
2-odd	15	2	2:14	1
2-odd	19	2	14:2	1
3-odd	17	3	3:13	2
3-odd	15	3	13:3	2
4-odd	21	4	4:12	1
4-odd	12	4	12:4	1
equal	35	8	8:8	1 & 2
homogenous	16	0	16:0	1 & 2
homogenous	16	0	0:16	1 & 2

Table 2: The top model set according to AIC, drawn from models including and excluding interaction terms. Terms in bold are significant at $p<0.05$ assessing the impact of individual terms in the model (table 3 & supplementary table 4).

Rank	Single variable terms	Interaction terms	df	AIC_C	ΔAIC_C
1	**Oddity status** Number odd **Position** Local density	**Oddity status * number odd** Position * local density	10	1274.018	0
2	**Oddity status** Number odd **Position** **Local density**	**Oddity status * number odd**	9	1275.100	1.081
3	**Oddity status** Number odd **Position** Local density	**Oddity status * number odd** Oddity status * local density Position * local density	11	1275.280	1.261
4	**Oddity status** Number odd **Position** Local density	**Oddity status * number odd** Number odd * local density Position * local density	11	1275.756	1.737
5	**Oddity status** Number odd **Position** **Local density**	**Oddity status * number odd** Oddity status * position Position * local density	11	1275.930	1.912
6	**Oddity status** Number odd **Position** Local density	**Oddity status * number odd** Position * local density Position * number odd	11	1276.011	1.993

Variance and standard deviation of random effects was <0.001 in the best-fitting model

Table 3: Model-averaged parameters from the GLMM output with attack status (target or not) as the response variable.

Fixed term	β	95% CI	ω_p	Z
(Intercept)	-3.883			
Position	**1.281**	**0.865, 1.697**	**1**	**6.033**
Local density	-0.104	-0.560, 0.352	1	0.446
Number odd	0.072	-0.031, 0.175	1	1.366
Oddity status	**1.049**	**0.453, 1.646**	**1**	**3.448**
Oddity * number odd	**-0.125**	**-0.234, -0.015**	**1**	**2.234**
Position * local density	0.309	-0.054, 0.805	0.82	1.262
Oddity * local density	0.019	-0.146, 0.378	0.16	0.273
Local density * number odd	0.001	-0.018, 0.031	0.13	0.169
Position * oddity	0.014	-0.589, 0.820	0.12	0.105
Position * number odd	< 0.001	-0.063, 1.697	0.11	0.049

Full model-averaged estimates (β), 95% confidence intervals (CIs), relative importance (ω_p) and Z are shown for all models appearing in the top model set ($\Delta AIC_C \leq 2$). Predictor CIs that do not overlap with zero are shown in bold. Candidate models: 66, top set models: 6 (see table 2).

Table 4 Binomial test output where the number of attacks to odd individuals were compared to what would be expected if odd shaded dots were targeted at random, with respect to overall group size and baseline probability (chance). Significance level is indicated by terms in bold, with * for p<0.05, ** for p< 0.01 and *** for p<0.0001***.

Treatment	# trials odd targeted in	total # trials	Expected probability	p
1 odd	9	31	0.063	**<0.001 ****
2 odd	9	34	0.125	**0.026 ***
3 odd	9	32	0.188	0.139
4 odd	11	32	0.25	0.154

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