

Original Article

Measuring marginal predation in animal groups

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Predation is a major pressure that shapes animal sociality, but predation risk is not homogenous within groups. Animals located on the group edge typically face an increased threat of predation, although different patterns have been reported. We created a simulation model to determine how changes in predator attack distance and prey density influence predation in relation to within-group spatial position. At large attack distances, peripheral animals were attacked far more than central animals. At relatively short attack distances, central individuals were attacked almost as often as peripheral animals. We used 6 different methods to classify within-group spatial position in our simulations and tested which methods were the best predictors of predation risk at different parameter values. The minimum convex polygon and angle of vulnerability methods were the best predictors of predation risk at large and medium attack distances, respectively. At relatively short attack distances, the nearest neighbor distance and neighbor density methods were the best predictors of predation risk. These patterns demonstrate that the threat of marginal predation is dependent on the behavior of predators and that for some predator-prey systems, marginal predation is predicted to be insignificant. We predict that social prey animals should change antipredatory behavior, such as vigilance, within-group spacing, and within-group spatial choice based on the relative distances at which their predators attack. These results demonstrate the importance of incorporating the behavior of predators in empirical studies and predator-prey models. *Key words:* attack distance, marginal predation, predation, predator behavior, vigilance, within-group spatial position. [*Behav Ecol* 22:648–656 (2011)]

INTRODUCTION

The risk of predation is an important factor shaping animal sociality. Animals in groups typically have lower predation risk than solitary individuals due to dilution, many-eyes, and confusion effects, but these benefits are not homogenous within the group (reviewed in: Krause and Ruxton 2002; Caro 2005). In general, individuals at the edge of the group experience higher predation risk (Hamilton 1971; Vine 1971; Krause 1994; Krause and Ruxton 2002). This latter effect, termed “marginal predation,” has been modeled and studied in a variety of predator-prey systems (Bumann et al. 1997; Viscido et al. 2001, 2002; Di Blanco and Hirsch 2006; Fernandez-Juricic and Beauchamp 2008; Morrell and James 2008). In contrast, some studies have not reported higher predation rates or predation threat at group edges, which may be due to the behavior of predators (Parrish 1989; Brunton 1997; Stankowich 2003). Lima (2002) raised the important point that in most systems little or nothing is known about predator behavior and without this knowledge it is difficult to model or determine the efficacy of antipredatory defenses.

Two of the earliest marginal predation models, Hamilton’s (1971) “Selfish Herd” and the models of Vine (1971) were based on considerably different assumptions. In the original selfish herd model, Hamilton (1971) used the example of lions hiding in tall grass and preying on wild cattle (following Galton 1871). Hamilton assumed that a predator could randomly appear at any point within the group and attack the closest individual. According to these assumptions, predation risk

should be closely linked to the density of neighbors and individuals spaced further from others are predicted to suffer higher levels of predation. This model used Voronoi polygons to calculate the area around each prey individual where a predator would be closer to the focal prey than to any other (termed “Domains of Danger”), which was assumed to correlate with predation risk. Because individuals at the edge of groups have unbounded Voronoi polygons, their Domains of Danger are, by definition, larger than central individuals thus resulting in higher levels of marginal predation. Even after mathematically correcting for unbounded polygons, the Hamilton model still holds, with peripheral individuals exhibiting higher predation risk and fewer close neighbors (Morton et al. 1994; Viscido and Wethey 2002; James et al. 2004).

In Vine’s (1971) model, marginal predation was not related to neighbor density (ND) but related to predators approaching prey animals from outside of the group. If a predator attacks the closest individual, individuals on the group edge are more likely to be attacked. This model assumes that predators do not pass up closer individuals in favor of more distant prey, which then reduces or eliminates the possibility of prey choice (Walther 1969; Temple 1987; Fitzgibbon 1990). Despite this assumption, these model parameters are likely more realistic than those of Hamilton in most predator-prey systems (James et al. 2004; Morrell and Romey 2008; Romey et al. 2008).

Hamilton’s (1971) assumption that predators can attack from any position within a group contrasts starkly with Vine’s (1971) assumption of predation from outside the group boundary. Both predation strategies are seen in the wild: a clear example comes from a study on nest predation in Least Terns (*Sterna antillarum*; Brunton 1997). The major nocturnal predator, the black-crowned night heron (*Nycticorax nycticorax*) enters the tern colony under the cover of darkness, which leads to increased predation in the center of the group. In

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contrast, American Crows (*Corvus brachyrhynchos*) approaching the colony during the day are unable to enter the group undetected (and are subject to mobbing by terns), thus restricting nest predation to the edge of the colony (Brunton 1997). Similar patterns are seen in mobile animal groups. Capuchin monkeys (*Cebus apella*) needed to approach within 2 m of an ocelot (*Leopardus pardalis*) model before reaching a 50% probability of detecting the predator (Janson 2007) demonstrating that ambush (sit-and-wait) predators could delay attack until a prey animal comes within a short strike distance, which may occur inside the group periphery.

The purpose of this study is 2-fold: First, we test how variation in the distance from which a predator launches its attack (predator attack distance) affects predation risk in relation to position of individuals within a 2D group. If predators are “pursuit” predators and attack individuals from relatively long distances, the first encountered animal should be on the group periphery. This should lead to higher predation risk for peripheral individuals. Alternately, sit-and-wait predators may attack from inside the group spread, thus within-group spatial position may not have a large affect on predation threat. In reality, predator attack distance falls along a continuum, and most prey species confront a diversity of predators (Sih et al. 1998; Relyea 2003; Broom et al. 2010). By creating a simulation model relating prey density and attack distance, we can determine how differences in predator attack distance lead to differential predation threat in relation to within-group spatial position. With this information, one can make predictions concerning how prey should change their behavior in response to particular predators or suite of predators.

Our second aim is to investigate the usefulness of different methods used to define spatial position in predicting risk to individuals within a group. One difficulty in comparing studies of predation on groups is that various studies have used different methods to specify individual position or expected risk. Here, we investigate 5 different measures of spatial position previously used to predict predation risk: distance from the center of the group (DTC), distance to the closest neighbor (nearest neighbor distance [NND]), the number of neighbors within a specific distance of a focal individual (ND), whether an individual is positioned on the vertices of the smallest convex polygon which encloses the group (minimum convex polygon [MCP]; Krause and Tegeder 1994), and the elliptical clock (EC) method which divides a group into 3 concentric ellipses. Some proposed methods are difficult or impossible for a researcher to use in the field; thus, the methods selected here were chosen because they have been implemented

in previous field studies: DTC—Balda and Bateman (1972); NND—Barta et al. (1997); Quinn and Cresswell (2006); ND—Hirsch (2002); Di Blanco and Hirsch (2006); MCP—Fitzgibbon (1990); Krause and Tegeder (1994); Brunton (1997); and EC—Robinson (1981); Janson (1990a, 1990b); Hall and Fedigan (1997). In addition, we introduce a new measure termed the “angle of vulnerability” (AoV, see Figure 1). We then determined which of the 6 methods had the best statistical fit to simulated predation data across a gradient of predator attack distances, group size, and prey density. This is similar to a previously used approach for determining the best method for recording within-group spatial position in relation to dominance (Christman and Lewis 2005). The results from our simulation model can be used by field biologists to choose the best method for measuring spatial position in their study system. In general, we predicted that methods which explicitly take into account group geometry (MCP, AoV, and EC) will be the best predictors of predation threat when predators attack from long distances and when prey live in large groups. At short attack distances, we predict that measures of local ND (NND and ND) will be better measures of individual predation risk.

Table 1
Tbl:1 Methodology used to calculate position values using each of the 6 different spatial position measures

Spatial position measure	Method of calculation
distance to center (DTC)	Firstly, we pinpoint the center of the group by taking the mean value of the <i>x</i> and <i>y</i> coordinates of each individual. We then calculate the distance from each individual to this point. For simplicity, we then categorize this distance into 20 equal categories (following Morrell and Romey 2008).
nearest neighbor distance (NND)	We calculate the distance between each focal individual and every other individual. NND is defined as the minimum of these values.
neighbor density (ND)	We count the number of individuals falling within D_N (the parameter defining the maximum distance used to calculate ND, here specified as $r/4$) of the focal individual.
minimum convex polygon (MCP)	We identify those individuals positioned on the MCP that encloses the group. These individuals are designated as “peripheral” and the remainder as “central.”
elliptical clock (EC)	Using the distance to center values calculated above, we determine the length of the group radius, divide this into 3 equal segments, and create 3 concentric circles. We use the distance to center values to specify which of 3 zones the focal individual falls into 1) center, 2) middle, and 3) edge.
angle of vulnerability (AoV)	We consider each individual in turn to be positioned at the center of a circle. We then imagine a line pointing directly “north” from that individual (i.e., if the individual were positioned at (0,0), we imagine a line pointing along the positive <i>y</i> axis). We then calculate the angle between that line and a line connecting the focal individual to each other individual. Sorting these angles in increasing order allows us to calculate the angle between adjacent individuals, moving in a clockwise direction around the focal individual. The largest of these values is the AoV. We then categorize the AoV into 1 of 4 categories (0°–90°, 90°–180°, 180°–270°, and 270°–360°).

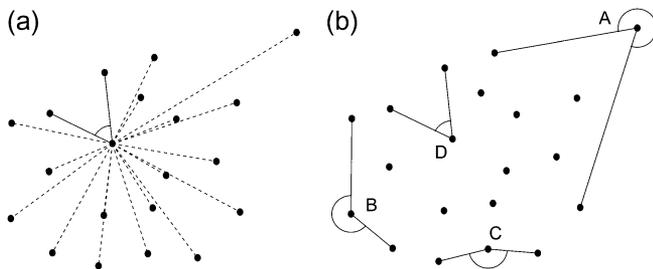


Figure 1
AoV method. (A) Dots represent animals from an overhead view of a group. The AoV is calculated by drawing straight lines between a target individual and all other group members. The largest unbroken angle, indicated with solid lines, yields the AoV value. (B) Circular segments around select individuals illustrate their vulnerability to direct attack from predators and thus their AoV values. AoV values for A = 300°, B = 230°, C = 160°, and D = 70°.

METHODS

Generating model groups

All simulations were performed in Matlab 2009b (Mathworks, Natick, MA), and for simplicity, we assume that groups are 2D and that predators attack in the same plane (i.e., do not attack from above or below the group, but from the side; see DISCUSSION). N point-like individuals were positioned within a circle at a given density, d . Individuals were placed at random by first selecting an angle from a uniform distribution between 0° and 360° and then a random distance from the center of the circle (0) to a maximum distance r (where $r = \sqrt{\frac{N}{d\pi}}$). Distances were selected as the square root of a distance picked from a uniform distribution between 0 and r^2 . This approach gives an even distribution of points within a circle (Baker and Zemel 2000), and we recorded the x and y coordinates for each individual. We then calculated 6 measures of spatial position for each individual in the simulated groups (Table 1).

Simulating predation risk

The predators appeared at a distance $4r$ from the group, at a position (P_S) determined by a randomly generated angle between 0° and 360° . The predator then moved toward a randomly generated location (the predator target, P_T) within the group using the same methodology used to position group members. A line (the predator path) connected the starting position (P_S) of the predator to the predator target (P_T) and continued through the group. Conceptually, this line reflects the path that the predator would take as it moved toward the group. We calculated the minimum distance to the predator path for each prey individual. Individuals within a distance a (the maximum distance from which a predator can successfully launch an attack) of this line were considered to be “at risk” of predation. Of these at risk individuals, the one positioned closest to the starting point of the predator (P_S), and therefore the one that would be encountered first, was attacked by the predator. If no individual fell within a of the line, the predator passed through the group without successfully launching an attack. Although we modeled predator–prey interactions in 2 dimensions, we assume that many of the resultant properties also hold for 3D groups. We simulated a total of $50N$ successful predation attempts on each group configuration, allowing us to calculate a risk of predation for each individual.

Measures of spatial position

The spatial position of prey individuals was calculated using each of the 6 spatial position methods programmed as listed in Table 1. All but one of the spatial position methods in the simulation models have been used in previous empirical studies (for additional methods and citations, see: Stankowich 2003). We created the AoV method to provide a more detailed measure of spatial position than the MCP method. The AoV is defined as the maximum angle in a radius around a focal animal in which a predator has direct access to the prey (in this respect, the method closely resembles the MCP method as described in Krause and Tegeder 1994). This angle is bounded by conspecifics, thus an individual may have several portions of its radius that are vulnerable to a predator, but only the maximum angle is used to record an animal’s AoV (Figure 1).

Linking risk to group position

We ran a simple regression analysis of risk of predation against each of the position measures, to generate R^2 values describing

how well each position measure predicts the risk of predation for individuals in that position. The use of linear regressions was not intended to provide a perfect fit for each method, but rather to provide a simple means of comparison between methods. We replicated the model 100 times for each parameter combination, to give a mean and standard error [SE] of the R^2 values. We identified the “best” position measure as the one with the highest mean R^2 value for each parameter combination. A large parameter space was chosen to reflect a wide diversity of patterns that could occur in nature. Group size (N) in our simulations varied from 20–100 individuals. Group density (d) ranged from $d = 0.5$ individuals in a circle with a radius of one (highly spread out) to $d = 5$ (tightly compact group). Predator attack distances (a) ranged from 0.1 to 1.6.

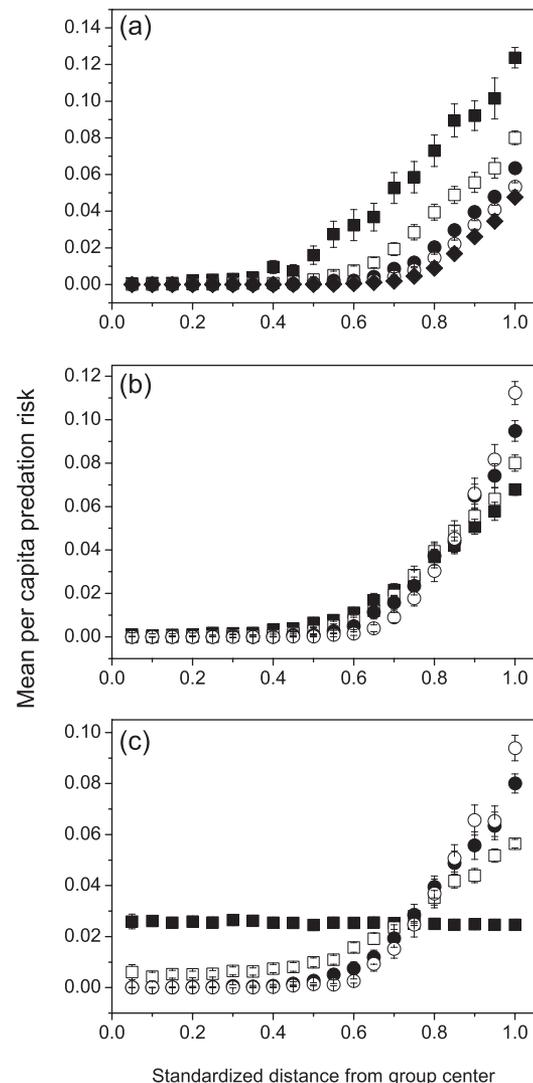


Figure 2 Mean (\pm 2 SE) per capita predation risk as a function of the standardized distance from the center of the group (see METHODS), illustrating the effect of varying each of the parameter values. (a) Altering group size (N): $N = 20$ (filled squares), $N = 40$ (open squares), $N = 60$ (filled circles), $N = 80$ (open circles), and $N = 100$ (filled diamonds). (b) Altering density (d): $d = 0.5$ (filled squares), $d = 1.0$ (open squares), $d = 2.0$ (filled circles), and $d = 5.0$ (open circles). (c) Altering predator attack distance (a): $a = 0.1$ (filled squares), $a = 0.5$ (open squares), $a = 1.0$ (filled circles), and $a = 1.5$ (open circles). Other parameters are $N = 40$, $d = 1$, and $a = 1$.

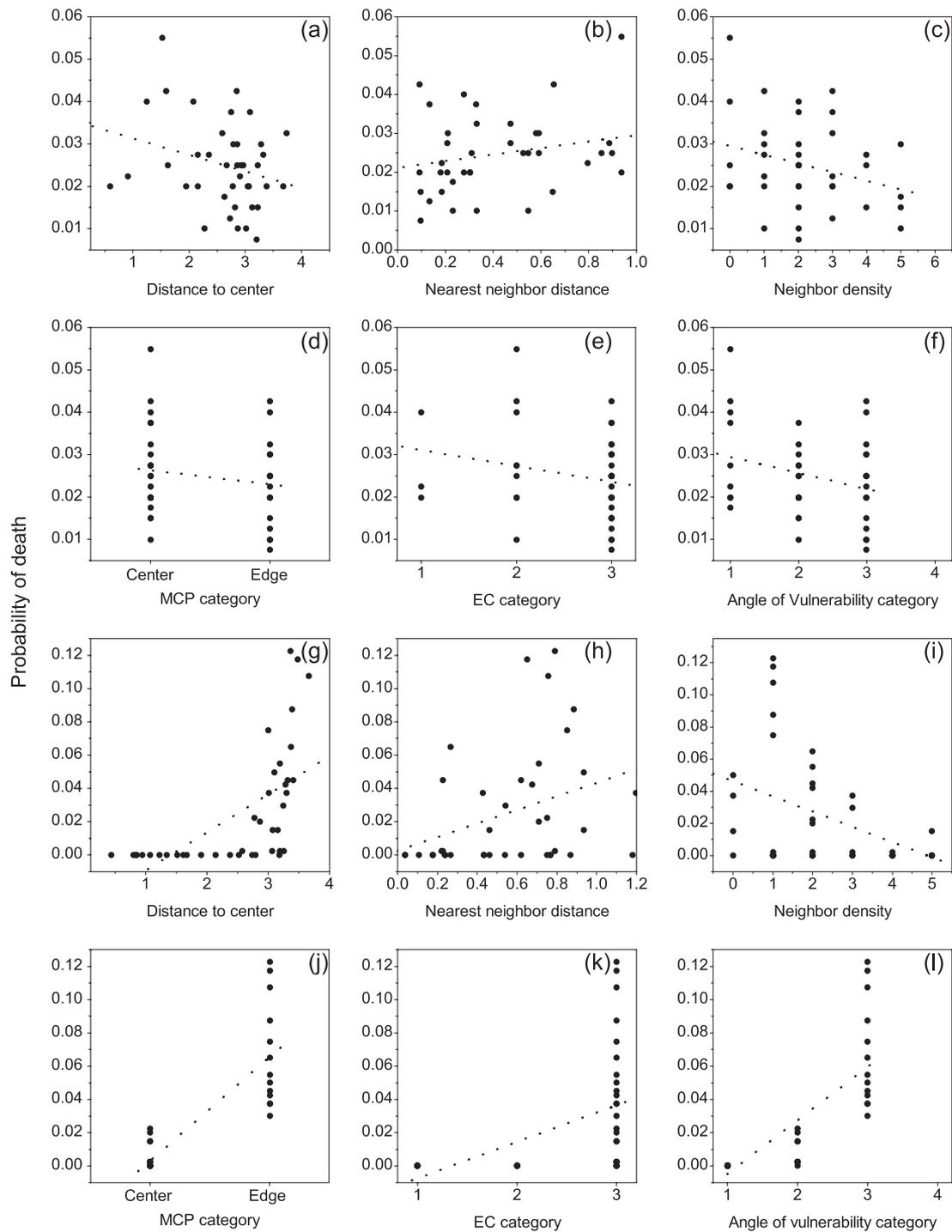


Figure 3

Examples of the relationship between position as measured by each of the different measures, for short predator attack distances ($a = 0.1$; top 6 panels) and long predator attack distances ($a = 1.5$; lower 6 panels), for a group of 40 individuals ($N = 40$) at a density $d = 1$. R^2 and P values are outlined in Table 2.

RESULTS

Predation risk and position within a group

In general, predation risk was higher for individuals that are positioned far from the group center (Figure 2). Risk was higher for individuals in small groups, as predicted by the dilution effect (Figure 2a), but critically, the distribution of risk between individuals close to the center and those close to

the edge depended on the distance from which predators can successfully launch an attack (Figure 2c). When predators exhibited a short attack distance ($a = 0.1$), risk was distributed more-or-less equally between all group members, regardless of spatial position. As attack distance increased, individuals further from the group center were at increased risk. At the longest attack distances (here, $a = 1.5$), only individuals on the outer edge of the group were at risk.

Table 2

Correlation coefficients and P values associated with the examples of the relationship between position (as measured using each different method) and predation risk illustrated in Figure 3, for short ($a = 0.1$) and long Predator attack distances ($a = 1.5$), for a group of 40 individuals ($N = 40$) at a density $d = 1$

Figure 3 panel	Predator attack distance	Method	R^2	Adjusted P
a	Short	DTC	0.0737	0.1201
b		NND	0.0671	0.1275
c		ND	0.0809	0.1130
d		MCP	0.0263	0.3180
e		EC	0.0514	0.1742
f		AoV	0.0814	0.1280
g	Long	DTC	0.3730	<0.0001
h		NND	0.1236	0.0522
i		ND	0.1626	0.0237
j		MCP	0.7171	<0.0001
k		EC	0.2330	0.0048
l		AoV	0.6491	<0.0001

Reported P values are adjusted using Benjamini and Hochberg's (1995) method for false discovery rate control. Significant P values are presented in bold font.

Assessing measures of spatial position

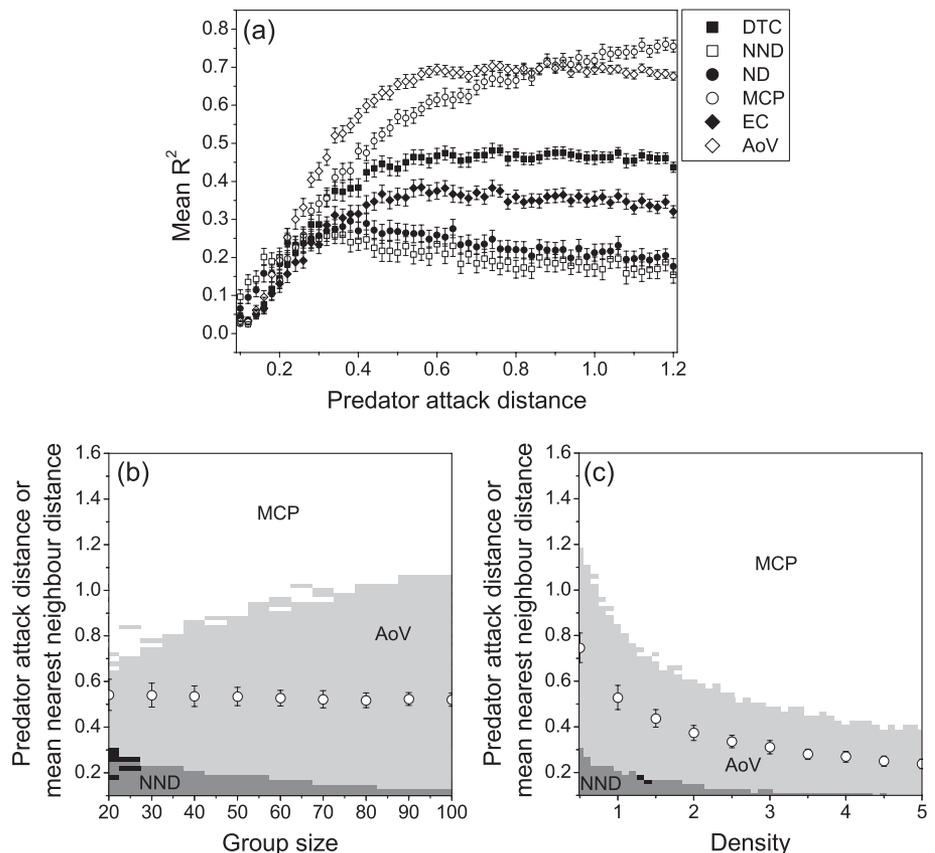
In our assessment of predation risk above, we only considered one measure of spatial position distance from the group center. Here, we consider all 6 measures. Different methods of assessing position in the group differed in their ability to predict the risk of predation for an individual in any given position, and this ability was affected by the size and density of the

group and the predator attack distance. Figure 3 and Table 2 show examples of the relationship between position and predation risk at 2 different predator attack distances: $a = 0.1$ and $a = 1.5$ for a group of 40 individuals ($N = 40$) at a density of 1 ($d = 1$). The first of these (Figure 3a–f) represents a predator which must be close to the prey before a successful attack can be launched and is therefore likely to attack from within a group (distances between nearest neighbors in a group of this size and density are 0.527 ± 0.044 [mean ± 2 SE]), whereas the second represents a predator attacking mainly from outside the group (Figure 3g–l). For short-attacking predators (Figure 3a–f), none of the methods of measuring spatial position were particularly good: in none of these examples was the relationship between position and risk significant (Table 2). For long-attacking predators, however, the spatial position measures were much better predictors of risk (Figure 3g–l). With the exception of NND ($P = 0.052$), all other methods led to statistically significant predictions of predation risk. In this particular example, MCP provided the best predictor ($R^2 = 0.717$) followed by AoV ($R^2 = 0.649$).

We next investigated in more detail the effect of predator attack distance (a), group size (N), and density (d) on the predictive power (mean R^2) of the different methods of assessing predation risk. There were clear differences between methods in their ability to accurately predict the predation risk of individuals (Figure 4a). At short predator attack distances, no method performed particularly well, as illustrated in Figure 4, although NND and ND performed slightly better than the other methods. MCP and AoV outperformed the other measures over most of the predator attack distances considered, with MCP performing the best at the longest predator attack distances. The worst-performing methods at long attack distances were those that measure local density

Figure 4

(a) The effect of predator attack distance on the mean (± 2 SE) R^2 value for the relationship between position (for each method) and predation risk over 100 replicate simulations. Parameter values were $N = 40$, $d = 1$, and $a = 1$. (b) Best measure of position by group size (N) and predator attack distance (a), at $d = 1$. White circles indicate mean NND (± 1 SE). (c) Best measure of position by density (d) and predator attack distance (a) for a group size (N) of 40. Shading in (b) and (c) indicates the best rule: white = MCP, light gray = AoV, dark gray = NND, and black = other rules (either ND or DTC). White circles indicate mean NND (± 1 SE)



(ND) and interindividual distances (NND; Figure 4a). Altering group size and density had little effect on these qualitative patterns (see Supplementary Material, Supplementary Figure S1).

Over the range of parameter space considered, different measures performed best at different parameter combinations. MCP and AoV were the best performing methods over most group sizes and predator attack distances (white and light gray areas, respectively in Figure 4b and c). At low predator attack distances, low group sizes, and low densities, marginal predation declined and NND was typically the best predictor of predation risk, although the low R^2 values indicate that NND was not a particularly good measure (dark gray in Figure 4b and c). Individuals with a close neighbor were at lower risk of predation than those whose closest neighbor was a greater distance away (Figure 2b). At the longest predator attack distances, MCP was the best predictor, whereas AoV outperformed MCP at medium/long predator attack distances. AoV and MCP performed best over the majority of the parameter space (Figure 4c, Supplementary Material, Supplementary Figures S1 and S2).

When group size was controlled for, the point at which the AoV method yielded smaller R^2 values than NND was linearly related to the NND/attack distance ratio. This transition point is also the approximate parameter value where marginal predation effects are predicted to decline precipitously. For a group of 40 individuals, when the mean NND was more than 2.5 times the predator attack distance, marginal predation dissipated and the AoV and MCP methods became poor predictors of predation threat (figure 4c). When group sizes were small ($N = 20$), the NND method yielded higher R^2 values at NND/ a ratios ≥ 1.8 , whereas at large group sizes ($N = 100$), the NND method yielded higher R^2 values at NND/ a ratios ≥ 4.3 .

DISCUSSION

Increased attack distance increases the degree of marginal predation

The degree of marginal predation in a group was directly related to the attack distance of the predator. At relatively large attack distances, predators almost exclusively attacked prey on the outer edge of the group. At short attack distances, the number of at risk individuals decreased, and thus, predators often attacked prey inside the group edge (Figure 2). In these cases, central individuals were unable to “hide” behind peripheral ones, as those peripheral ones fell outside the attack range of the predator as it approached the group. Although some empirical studies have reported that predators preferentially attacked central group members (Parrish 1989; Brunton 1997; Ioannou et al. 2009), most studies have reported strong marginal predation effects (reviewed in: Krause 1994; Krause and Ruxton 2002; Stankowich 2003; Caro 2005). The absence of marginal predation effects in some empirical studies may be due to behaviors, such as preferential targeting of central individuals, confusion effects, or targeting of phenotypically distinct individuals, in addition to the short attack distances modeled here (Krause and Ruxton 2002). Our model demonstrates that if we eliminate these complicating factors and predators simply attack the closest prey, relatively short attack distances will result in an almost complete negation of the marginal predation effect. It is therefore essential that researchers know something about predator behavior when studying or modeling the effects of predation threat on prey behavior. We believe that studies relating feeding and predation tradeoffs to spatial position need to demonstrate that peripheral spatial positions are more dangerous or determine what type of hunting patterns are exhibited by the predators (Romey 1995; Morrell and Romey 2008; Hirsch 2011a, 2011b).

The effectiveness of spatial position methods depends on attack distance

Stankowich (2003) outlined several problems with the use of various methods for determining spatial position and noted that the most appropriate measure of spatial position may differ depending on the study system. Our study is the first to test the efficacy of different methods in a predation simulation model. In the majority of our model parameter space, the AoV and MCP methods resulted in the highest R^2 values, thus were the best predictors of predation threat. At the upper limits of attack distance, MCP was always the most effective measure of predation risk, followed closely by the AoV. At intermediate attack distances, the AoV method worked slightly better than the MCP. Given the possibility that edge individuals can sometimes have high ND values due to a random distribution of individuals, density based methods (ND and NND) are less direct measures of predation threat than the AoV and MCP methods. This model demonstrates that for many predator-prey systems, the AoV or MCP methods are the best measures of predation risk.

Even though the MCP and AoV measures are similarly constructed methods, there are advantages and disadvantages related to both. Because the MCP method is a zero-one variable, it will have fewer degrees of freedom than the categorical AoV method and thus should have been a statistically better measure. On the other hand, the AoV method is ultimately a continuous variable which we broke up into 4 categories because we believe that recording precise AoV angles in field conditions may be difficult or time consuming. The AoV measure provides more detail about predation threat to individuals, which are located just inside the group edge than the MCP method. For the example in Figure 1, the MCP method considers individuals C and D (from Figure 1) to be in the same category, even though their risk of predation may be quite different, especially at medium-short predator attack distances. In our simulations, few if any individuals fall into the largest AoV category (270° – 360°). In natural systems and in species with smaller group sizes (<20), individuals might be more likely to fall into this last category. Additionally, one could use the largest AoV category to define “solitary” individuals (see DISCUSSION in: Stankowich 2003). The AoV method can be easily recoded as a MCP measure and not vice versa, thus we strongly recommend the use of the AoV method in future studies of marginal predation.

At smaller attack distances, the NND method was typically the best predictor of predation risk, followed closely by ND. In general, when the attack distances were short, these 2 measures of local density worked better than the AoV and MCP methods. This result confirms predictions that as attack distance decreases, and predators are able to enter prey groups, the density of close neighbors should be the primary determinant of predation risk, and not whether the prey are located on the periphery of the group (Hamilton 1971). Alternately, because R^2 values for all 6 methods were low at short attack distances, it could be concluded that no measure of spatial position is a good predictor of predation threat at small predator attack distances. Empiricists should note that when choosing a methodology for recording within-group spatial position, it is important to have some knowledge of the attack strategies of predators (sit-and-wait vs. pursuit predators) or an approximate measure of the ratio between attack distance and interindividual spacing within the prey group.

Even though the use of the EC method never resulted in the highest R^2 values in our parameter space, this is the only method that includes a built in measure of group directionality (although we did not consider group movement here).

Given that several empirical studies have found that predation threat is highest at the front edges of mobile groups, the EC method may be the preferred method for some studies (Janson 1990b; Bumann et al. 1997; Carbone et al. 2003; Di Blanco and Hirsch 2006; Romey and Galbraith 2008). A better method might be to record centrality according to the AoV or MCP methods while simultaneously recording group directionality in a manner similar to the EC method. It remains to be tested if adding a directionality component to the AoV or MCP methods would result in higher R^2 values in a system with directional predation threat.

Group density is positively related to marginal predation

When all other variables were controlled for, as individuals spaced together more closely the degree of marginal predation increased (Figure 2b). As individuals in a group spread out, the likelihood of a predator entering the group for an attack increased, although density affected marginal predation less than attack distance and group size (Figure 2). We expect that in many animal groups, density will likely covary with group size, with individuals in larger groups being spaced closer together. Because of this, we controlled for ND in our simulations so that NND did not decrease with increasing group size (Figure 4b). If group size is kept constant, a monotonic nonlinear relationship exists between density and marginal predation (Figure 4c). This pattern arises because the mean linear distance between closest group members (NND) is exponentially related to the number of individuals within a given radius of prey individuals (d). When marginal predation is reconsidered as a function of mean NND attack distance, more predictable results arise. For a given group size, there is a direct linear relationship between the point at which the AoV method yielded smaller R^2 values than NND and the NND/a ratio. This is also the point at which significant marginal predation effects should start to break down.

The NND and attack distances used in this model were not based on empirical data but are unitless values used to test the relative affects of group size, density, and attack distance on levels of marginal predation. These values can be converted into meters or the appropriate unit of measure for a given study system. For example, if a predator generally attacks prey at a distance of 25 m, this would be a large attack distance for a group of 40 individuals spaced 10 m apart on average (NND/a ratio = 0.4), whereas it would be a short attack distance for 40 animals spaced 100 m apart (NND/a ratio = 4). Because this relationship between the mean NND/a and marginal predation is affected by group size, the precise point at which marginal predation is predicted to decline cannot be determined through a simple rule (such as a multiple of interindividual distances). When choosing a method for a particular study system, it is important to consider group size, and the average interindividual distance between prey individuals in relation to the predator attack distance. Although we recommend using the AoV method in most cases, we also encourage field biologists to use more than one measure of spatial position (AoV combined with the NND or ND) especially when NND/a ratios are high.

How should attack distance influence prey behavior?

This model leads to several predictions about how social animals should respond to different types of predators. When prey are only threatened by pursuit predators, individuals should try to locate themselves on the inside of the group edge. Feeding competition and social interference may force some individuals to the group edge (Janson 1985; Romey 1997; Hemelrijk

2000; Hirsch 2007), but if an animal desires protection from predation, the most effective spatial defense against pursuit predators is to be located more centrally. For prey threatened by sit-and-wait predators, having a high ND should be a more effective antipredatory defense than being located inside the group periphery (but see Ioannou et al. 2009). If prey animals seek to increase their number of close neighbors, this behavior may lead to an increase in group clustering. Many species have been observed temporarily ranging in small subgroups or foraging parties which would be an effective defense against sit-and-wait predators while simultaneously reducing feeding competition (Owens and Owens 1978; Smolker et al. 1992; Norconk and Kinzey 1994; Gompper 1996). Another example is that several studies have found higher prey densities at the front edges of groups (Bumann et al. 1997; Di Blanco and Hirsch 2006; Quinn and Cresswell 2006). If predation threat is highest at the front edge of the group, increasing the density of conspecifics in this area of the group would be a good strategy to reduce the risk of predation from sit-and-wait predators.

A common response to increased predation threat is for animals to scan their environment for predators (reviewed in: Elgar 1989; Caro 2005). Prey vigilance rates have often been used as a proxy for predation threat. It may be possible to determine whether prey face a larger threat from sit-and-wait versus pursuit predators based on whether vigilance rates respond more to local measures of ND or within-group spatial position. Unfortunately, very few studies have recorded both variables in relation to vigilance rates (see: Hirsch 2002; Di Blanco and Hirsch 2006; Quinn and Cresswell 2006; Fernandez-Juricic and Beauchamp 2008). Another complicating factor is that antipredatory vigilance may be differentially effective depending on predator hunting style. In the case of sit-and-wait predators, some predators are able to approach prey so closely that most antipredatory vigilance would be ineffective at detecting a predator before it is within attacking distance (Boinski et al. 2003). This leads to the conclusion that studies using antipredatory vigilance as a proxy for predation threat may be measuring the threat from pursuit predators but not from sit-and-wait ambush predators.

The distance at which predators attack has an overriding influence on the antipredator defenses available to prey. In the case of sit-and-wait predators, by the time the prey detects the predator, the predator may have already started the attack. In this case, there are few options available to deter predation other than fleeing from the predator. In cases where a sit-and-wait predator is seen before an attack, prey will often give alarm calls, which can act to warn conspecifics and signal predator detection. These alarm calls may deter predators from pursuing knowledgeable prey animals (Zuberbuhler et al. 1999; Clark 2005; Wheeler 2008). On the other end of the spectrum, pursuit predators which attack from large distances are much more likely to be discovered before they start an attack, especially in open environments. This allows prey more time to react to the predator before the predator reaches the group and increases the amount of antipredatory behavioral strategies available to the prey (Ydenberg and Dill 1986). In these cases, prey can move away from the predator and toward conspecifics before the predator reaches the group margins (Morrell and James 2008; Morrell et al. 2011a, 2011b). This can lead to changes in group geometry which have been studied in detail by Viscido and colleagues (Viscido et al. 2001; Viscido and Wethey 2002). If a refuge is nearby, prey animals can flee to these areas to provide protection from predators. Prey can also signal their health or physical stamina to predators in hopes that the predator will not attack (Caro 1986a, 1986b, Stankowich and Coss 2007).

What factors influence predator attack distance?

The distance at which prey should flee from a predator has been well studied and modeled, but much less is known about what factors influence the distance at which predators detect and attack prey (Ydenberg and Dill 1986; Lima 2002; Broom and Ruxton 2005; Cooper and Fredrick 2007). As a predator approaches its prey, or vice versa, the likelihood that the predator is close enough to capture the prey should increase. On the other hand, as predator and prey approach each other, the probability that the prey animal will detect the predator should increase (Broom and Ruxton 2005). The distance at which prey can detect a predator could then limit the potential attack distance of the predator. For example, if a sit-and-wait predator is detected by their prey before an attack, the predator will have lost its surprise advantage, which should reduce the effectiveness of the attack.

In the current model, we assumed that predators chose their closest target and that all prey are identical, which eliminates the possibility of prey choice. This assumption is violated by predators that preferentially target small, weak, or injured animals (Stankowich 2003; Genovart et al. 2010). On the other hand, the predator attack distance may influence the ability of animals to target prey. In open habitats, where predators are able to observe prey from a distance, it may be easier to see visible signs of prey vulnerability (but see: Cresswell et al. 2003). In these cases, pursuit predators may pass up closer prey to attack central vulnerable animals. In the case of sit-and-wait predators, it may be less important for them to select vulnerable prey because their use of surprise would allow them to approach within striking distance of prey, before the prey have sufficient time to evade the predator. It may be possible for a well-hidden predator to allow some animals to pass close by without being attacked while waiting for more vulnerable individuals. This may be advantageous in cases where large adult prey are difficult to take down while smaller, younger individuals are easier to catch and kill.

Many animal groups move in 3, rather than 2 dimensions. We believe that the general results from this 2D model should still hold in 3D systems, but this may result in more complex predator-prey encounters. For example, it is plausible that targeting prey individuals in a large 3D group is more cognitively challenging than in our 2D model, thus prey choice may be influenced by confusion and oddity effects (Krakauer 1995; Ioannou et al. 2008). Even in cases where 3D predators attack 2D prey (such as raptors attacking shore birds, or fish predators attacking surface-dwelling insects), predators have been observed attacking the group margins and not just the closest prey individual (Quinn and Cresswell 2006; Romey et al. 2008). This result helps illustrate the fact that predator-prey interactions are complex, and this simulation model cannot address all of the factors that influence a predator's choice of prey.

Ideally, predator attack distances should be greater than the distance at which the prey generally detects the predator. Unfortunately, remarkably little is known about predator detection distances in relation to attack distances (Caro 2005). Given the importance of predator attack distance in relation to marginal predation risk, we believe that more experimental and empirical work should be done to investigate predator attack distances and predator-prey detection distances. Although predators have been observed using a wide variety of methods to elude detection (hiding behind foliage, standing motionless, hunting downwind, etc.), very little work has quantified the efficacy of these behaviors with respect to predator detection or attack distances (Funston et al. 2001; Cresswell et al. 2010).

SUPPLEMENTARY MATERIAL

Supplementary material can be found at <http://www.beheco.oxfordjournals.org/>.

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