



# Marginal predation methodologies and the importance of predator preferences

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Biologists have studied group dynamics and attempted to define the benefits of gregariousness across diverse taxa for several decades. The relative costs and benefits of group living (reviewed in Krause & Ruxton 2002) may differ between group members so that each is under selection to maximize its individual fitness in different ways (Rubenstein 1978). For example, individuals on the edge of a group may have higher feeding rates but suffer higher predation risk, whereas those on the inside enjoy lower rates of predation but suffer reduced feeding rates (e.g. colonial spiders: Rayor & Uetz 1990). Many years ago ornithologists studying predation rates in colonial-nesting birds reported that predation rates on eggs or fledglings were higher for solitary nests outside of the colony than for those inside the colony, and positions on the periphery of the colony were more susceptible to predation than central positions (e.g. Taylor 1962; Kruuk 1964; Patterson 1965). This phenomenon of differential predation risk within a group (i.e. a greater risk of predation on the periphery relative to the centre) is known as 'marginal predation'. Similar early studies found the same phenomenon of differential risk in mobile animals (e.g. mammals: Galton 1871; birds: Wynne-Edwards 1962). Following these early studies, several mathematical and geometrical models of the benefits of group formation emerged, the most famous of which is Hamilton's (1971) theory of the 'selfish herd', in which aggregations of animals form purely by selfish behaviour of individuals. Hamilton's (1971) predictions were echoed and extended by Vine (1971) and since have been refined and formalized by computer models to show how within-group movements of individuals during attacks may minimize their individual predation risk (e.g. Morton et al. 1994; Gueron et al. 1996; Barta et al. 1997; Beecham & Farnsworth 1999; Viscido et al. 2001). While Hamilton's (1971) ideas have been the inspiration behind most of the theoretical issues at hand, the problem with analysing the empirical validity of these models is that we do not have standardized methodologies for measuring marginal predation and benefits of aggregation.

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Hamilton's (1971) selfish herd theory has sparked many studies of differential individual fitness within groups (for reviews see Mooring & Hart 1992; Krause 1994; Krause & Ruxton 2002). While vigilance has been used in the past as an indicator of predation risk to study benefits of increased group size (e.g. Hoogland & Sherman 1976), there is little empirical evidence that central individuals scan less because they are safer than peripheral individuals, although some species have been found to increase their level of vigilance with increasing distance from safe locations (e.g. house sparrows, *Passer domesticus*: Barnard 1980; dark-eyed juncos, *Junco hyemalis*: Caraco et al. 1980). Studies that quantify actual rates of attack and capture are better indicators of risk in groups of prey. Most of these studies have detected differential risk resulting from marginal predation (see Table 1): only a handful of studies that have directly measured predation on groups have found that peripheral animals are not at greater risk than central animals (e.g. birds: Quinlan 1983; Apa et al. 1997; Brunton 1997; fish: Parrish 1989; Parrish et al. 1989). The presence of a centre-edge effect depends on not only the geometry of the group, but also on the place of origin of the predatory attack: an avian predator attacking a two-dimensional group from above may not show the same centre-edge effect that a terrestrial predator would.

Studies directly measuring spatial differences in predation risk within groups (two-dimensional and three-dimensional) of several taxa (e.g. insects, fish, birds, mammals) are not uniform in how they define certain aspects of the group and many periphery-centre definitions are highly susceptible to misclassification. Predation terminology and operational definitions of within-group spatial classifications differ between these studies, making comparisons of per capita predation rates nearly impossible across studies. Comparing predation risks reveals the relative degree to which one source of natural selection (predation) favours group formation and group maintenance, and we can determine whether group formation is an adaptive response to active predation, or to other ecological conditions (e.g. patchy food distribution, byproduct of the mating system, etc.), or both.

Table 1. Different uses of 'periphery' and 'centre' in the literature and examples of studies that applied these different terminologies

Technique	Reference	Species	Group type	Relative predation risk
Polygon vertices	Krause & Tegeder 1994 Barber & Huntingford 1996 Brunton 1997 Fitzgibbon 1990 Colagross & Cockburn 1993	Three-spined stickleback, <i>Gasterosteus aculeatus</i> Minnow, <i>Phoxinus phoxinus</i> Least terns, <i>Sterna antillarum</i> Thomson's gazelles, <i>Gazella thomsoni</i> Grey kangaroo, <i>Macropus giganteus</i>	Fish school Fish school Nesting colony Mammal herd Mammal herd	Periphery>Centre Periphery>Centre Centre>Periphery Periphery>Centre Periphery>Centre
Layers of protection	Parrish et al. 1989 Rayor & Uetz 1990 Rayor & Uetz 1993 Gross & MacMillan 1981 Yorio & Quintana 1997	Flat-iron herring, <i>Harengula thrissina</i> Spider, <i>Metopeira incrassata</i> Spider, <i>Metopeira incrassata</i> Bluegill sunfish, <i>Lepomis macrochirus</i> Terns, <i>Sterna maxima</i> ; <i>S. eurygnatha</i>	Fish school Nesting colony Nesting colony Nesting colony Nesting colony	Periphery=Centre Periphery>Centre Periphery>Centre Periphery>Centre Periphery>Centre
Surrounded on all sides	Parrish 1989 Veen 1977 Tenaza 1971 Foster 1989	Atlantic silversides, <i>Menidia menidia</i> Sandwich terns, <i>Sterna sandvicensis</i> Adélie penguins, <i>Pygoscelis adalae</i> Pacific sergeant major damselfishes, <i>Abudefduf troschelii</i>	Fish school Nesting colony Nesting colony Nesting colony	Centre>Periphery Periphery>Centre Periphery>Centre Periphery>Centre
Distance from 'edge'				
Thickness and degree of trampling of vegetation on lek	Trail 1987 Wiley 1973 Balmford & Turyaho 1992	Guianan cock-of-the-rock, <i>Rupicola rupicola</i> Sage grouse, <i>Centrocercus urophasianus</i> Uganda kob, <i>Kobus kob thomasi</i>	Bird lek Bird lek Mammal lek	Periphery=Centre Periphery=Centre Periphery>Centre
Central circle and two concentric rings of equal area	Balda & Bateman 1972	Piñon jay, <i>Gymnorhinus cyanocephalus</i>	Nesting colony	Periphery>Centre
Mean distance to centre of colony as boundary	Balda & Bateman 1972	Piñon jay, <i>Gymnorhinus cyanocephalus</i>	Nesting colony	Periphery>Centre
Intensity of swarm shadow on bottom of tank	Jakobsen & Johnsen 1988	Water flea, <i>Bosmina longispina</i>	Insect swarm	Periphery>Centre
No formally stated definition given	Taylor 1962 Schaller 1964 Horn 1968 Hoogland & Sherman 1976 Buckley & Buckley 1977 Fuchs 1977 Apa et al. 1997	Adélie penguins, <i>Pygoscelis adalae</i> White pelican, <i>Pelecanus erythrorhynchos</i> Brewer's blackbird, <i>Euphagus cyanocephalus</i> Bank swallow, <i>Riparia riparia</i> Terns: <i>Sterna maxima</i> ; <i>S. eurygnatha</i> Sandwich terns, <i>Sterna sandvicensis</i> Sharp-tailed grouse, <i>Tympanuchus phasianellus columbianus</i>	Nesting colony Nesting colony Nesting colony Nesting colony Nesting colony Nesting colony Nesting colony	Periphery>Centre Periphery>Centre Periphery=Centre Periphery>Centre Periphery>Centre Periphery>Centre Centre>Periphery
	Lindström 1989 Mulhare & Maignan 1998	Finches, <i>Fringilla coelebs</i> ; <i>F. montifringilla</i> Mongolian gerbils, <i>Meriones unguiculatus</i>	Bird flock Mammal colony	Periphery=Centre Periphery>Centre

By comparing studies demonstrating significantly greater risk in peripheral positions and studies demonstrating significantly greater risk in central positions, I show that there are problems with how researchers measure differential risk within animal groups, and that often there are subtle but important consequences of choosing a particular set of definitions of marginal predation. Also, issues such as predator hunting methods and preferences for prey size/class are extremely important to the understanding of predation on groups. The question arises as to whether differential predation rates between positions within groups are merely correlates of individual spatial organization (e.g. according to age, size, sex, rank: [Rayor & Uetz 1993](#)) and/or predator biases for particular prey phenotypes (e.g. juveniles, injured individuals, older individuals: [Walther 1969](#)). Likewise, [Lima \(2002\)](#) claims that predators have been largely ignored from the predator-prey interaction. After considering the ramifications of allowing predators to respond strategically to prey behaviour in models of predator-prey interactions, he advocates allowing predators to move and respond to prey movement in such models. Extending this suggestion further, I recommend approaching the problem of predation on groups while considering predator preferences for (or restrictions to) specific prey sizes/classes and the effects of multiple species of predator, or risk spurious conclusions regarding spatially differential predation risk.

My goals here are to demonstrate: (1) that variation in marginal predation terminology hampers attempts to determine objectively whether some positions within a group are really more dangerous than others, (2) that inconsistent and subjective categorization of individuals as 'in a group' or 'out of a group' further amplify these problems, and (3) that future studies of marginal predation must take into account multiple species of predators and predator biases for certain prey types.

### Defining Regions Within Groups

Because defining group membership and group size can be a difficult task in itself (see below), I will first discuss the problems of defining regions within groups. To demonstrate the quantitative and qualitative problems that can arise when using different definitions of periphery and centre, I present two spatially different, hypothetical animal groups, each with membership of 'periphery' and 'centre' classified according to four definitions of group membership used in published studies (see below; [Figs 1a–d, 2a–d](#)). Although I chose spacing of individuals within the groups to illustrate the differences between these definitions, these classifications also represent biologically relevant group formations. [Figure 1](#) shows a tightly packed group of individuals possibly resembling a colony of nesting birds. [Figure 2](#) shows a more diffuse group of individuals, changing in density from centre to edge, possibly resembling a herd of ungulates.

#### Definitions of group membership

(1) *Polygon vertices*. These can be defined in two ways that give the same result. (a) An animal is peripheral if it

is 'at the vertex of the smallest closed convex polygon enclosing all members of the [shoal]' ([Krause & Tegeder 1994](#)). (b) An animal is peripheral if it 'had no group members within a semicircle (180°) on one side of [it]' ([Fitzgibbon 1990](#)). This is one of the most commonly accepted and frequently used classification systems ([Krause & Ruxton 2002](#)).

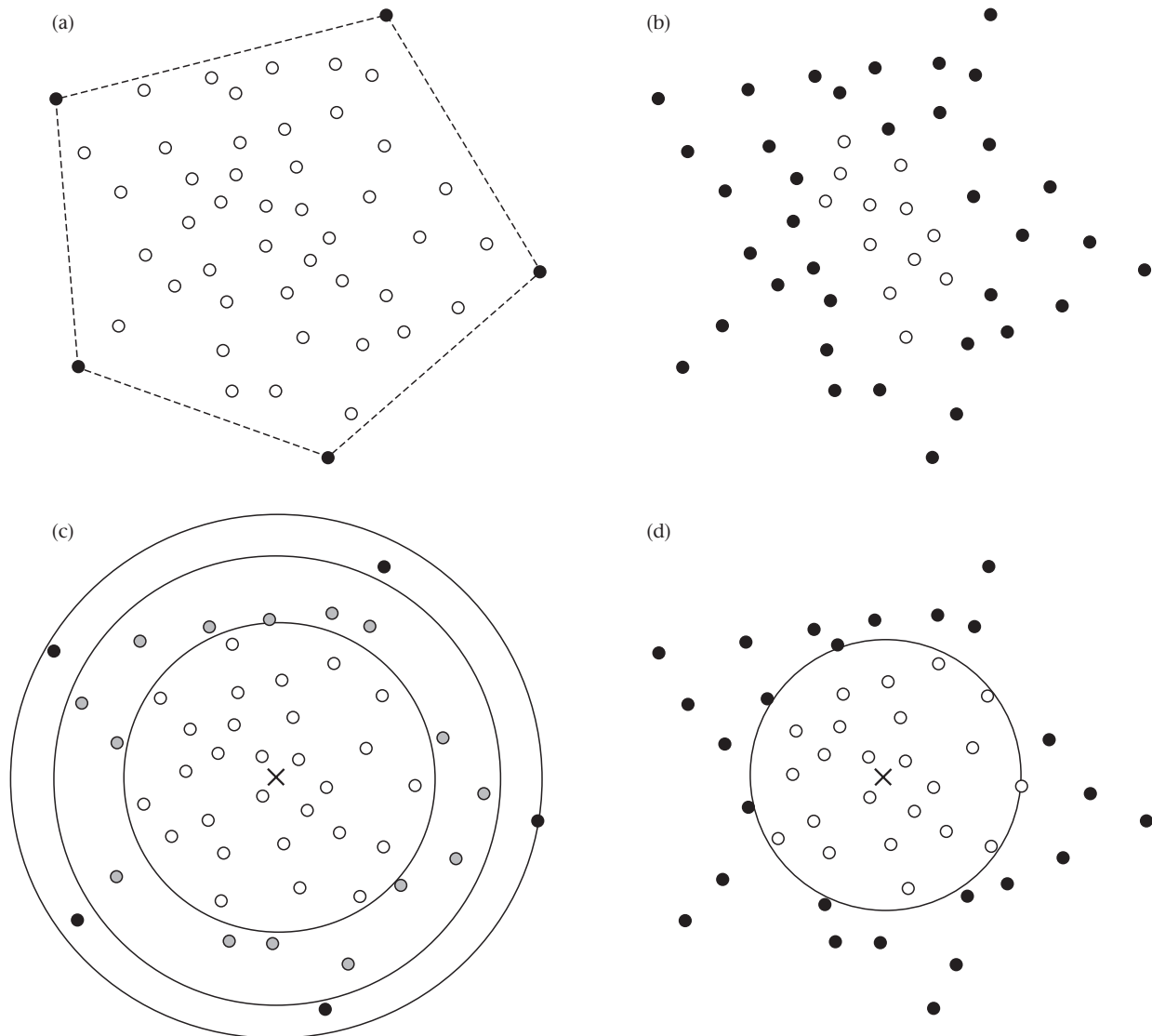
(2) *Layers of protection*. Individuals are central if they are entirely enclosed by  $n$  layers of other group members ( $n$  varies from study to study; 2–3 layers are shown in [Fig. 1b](#) after [Rayor & Uetz 1990](#)).

(3) *Concentric circle*. A circle is drawn around the entire group, and the area within that circle is divided into two concentric rings and a centre circle, all of equal area; peripheral animals occur in the outermost rings (which rings constitute the 'periphery' was not specified so I will use both) and central animals are enclosed in the centre circle ([Balda & Bateman 1972](#)).

(4) *Mean distance to centre*. The distance of each individual from the geographical centre of the colony is measured and the mean distance is calculated; this mean distance is then used as the boundary between centre and periphery ([Balda & Bateman 1972](#)).

In the star-shaped group resembling a colony of nesting birds ([Fig. 1a–d](#)), there is great variation between these definitions in how individuals are categorized as 'peripheral'. Only the individuals making up the five points of the star are peripheral in polygon vertices ([Fig. 1a](#); 43 central); this definition of peripheral is 'strict', because other individuals that are on the edge of the colony but between the vertices are defined as central but are more exposed to predation than those closer to the geographical centre. The layers of protection definition ([Fig. 1b](#)) is the most 'permissive', with 36 individuals being defined as 'peripheral' (12 central); using a definition this permissive might show a nonsignificant difference between predation rates on central and peripheral individuals, because some of the individuals defined as peripheral are really well protected and at little risk of predation relative to those on the edge. The mean distance to centre ([Fig. 1d](#)) and concentric circles ([Fig. 1c](#)) definitions are intermediate in the number of individuals classified as peripheral.

In the diffuse group resembling a herd of ungulates ([Fig. 2a–d](#)), we see very different results when different definitions are imposed. Here, polygon vertices ([Fig. 2a](#)) and concentric circles ([Fig. 2c](#)) are the strictest definitions, only categorizing seven and nine individuals, respectively, as peripheral (with 73 and 71 central individuals, respectively). These definitions may give a false impression of marginal predation, because only the extreme edge individuals who should suffer the greatest predation are counted as peripheral; many individuals near the central/peripheral border that are classified as central may also incur a relatively large predation risk.



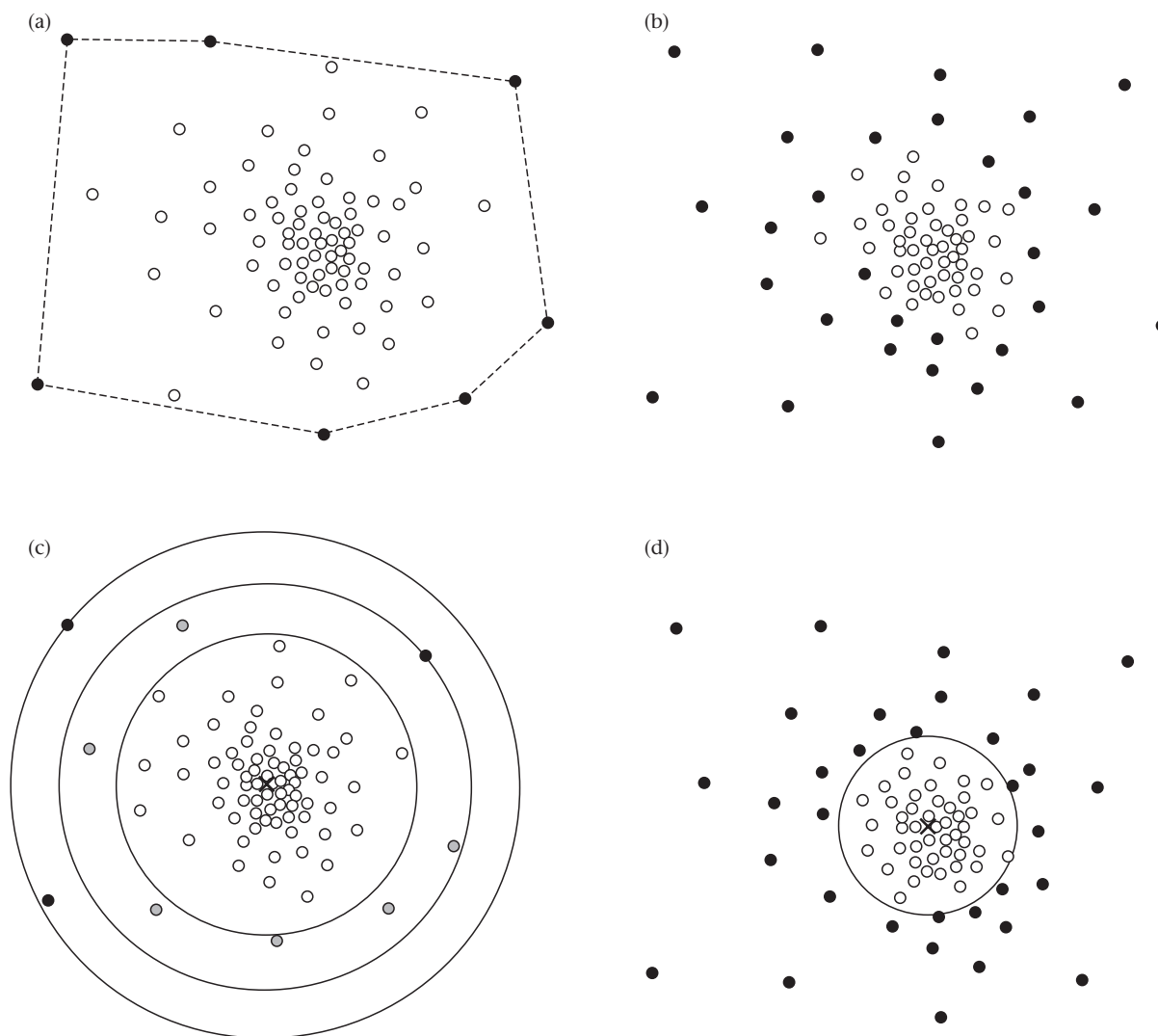
**Figure 1.** Fictional animal group of tightly packed individuals defined according to: (a) polygon vertices; (b) layers of protection ( $N=2-3$ ); (c) concentric circles (individuals in the second ring are coloured grey but are included as peripheral); and (d) mean distance to centre (=the mean distance to 'X'). ●: Peripheral individuals; ○: central individuals.

Layers of protection (Fig. 2b) and mean distance to centre (Fig. 2d) result in very permissive categorizations with 30 and 34 peripheral individuals, respectively (50 and 46 central individuals, respectively). All of these definitions, specifically the popular polygon vertices and layers of protection, suffer from potential misclassification of individuals, and, depending on the true spatial distribution of predation risk and the size of the group, different definitions could result in varying conclusions about the existence of marginal predation.

From these figures, a serious problem emerges regarding how to judge results of marginal predation experiments that use different definitions: strict definitions may misclassify some individuals that are at high risk as central, and permissive definitions may classify individuals that are fairly well protected from predation by several layers as peripheral. The definitions illustrated

here are just a sample of the most utilitarian (polygon vertices and layers of protection) and most mathematical (concentric circles and mean distance to centre) definitions from the large pool of definitions used in past studies of marginal predation. Table 1 shows additional examples of definitions that biologists have used to define grouped individuals as 'peripheral' and 'central'. Through both direct (attack, capture rates) and indirect (e.g. breeding success) measures of predation risk, the majority of studies show that individuals occupying peripheral positions are in greater danger of predation than are central individuals.

Many definitions are methodologically difficult to carry out, are open to subjective interpretation, or require detailed spatial data. Veen (1977, page 40) defines a central position in a sandwich tern, *Sterna sandvicensis*, colony as 'surrounded by neighboring nests at all sides'



**Figure 2.** Fictional animal group of individuals diffusing away from the centre and defined according to: (a) polygon vertices; (b) layers of protection ( $N=2-3$ ); (c) concentric circles (individuals in second ring are coloured grey but are included as peripheral); (d) mean distance to centre (=the mean distance to 'X'). ●: Peripheral individuals; ○: central individuals.

and surrounded by three or more nests. Rarely do neighbouring individuals fall into an ideal hexagonal arrangement around a focal individual, leaving a difficult decision for the biologist as to whether an individual is truly 'surrounded' and how close another individual must be before it counts as a 'neighbour'. Perhaps providing an approximate maximum angle of exposure to the exterior of the group would help to standardize this classification scheme (e.g. if an individual is surrounded by three individuals, then the maximum angle =  $120^\circ$ ; if an individual is surrounded by six individuals, then the maximum angle =  $60^\circ$ ). Many definitions that are based on spatial measurements and geometry (e.g. mean distance to centre and concentric circles) require an overhead (aerial) picture of the group and time-consuming calculations to define the peripheral and central regions of the group.

In terrestrial lekking species, the most common way to classify individuals is by recording the location of their

territories on the lek and the height of grass on the territory, where central territories have greater trampling of grass (Table 1). This classification protocol seems to be both adequate and appropriate for terrestrial lekking species; however, a cutoff height of vegetation should be set prior to data collection and reported in the results. None of the three studies of terrestrial lekking species listed in Table 1 reports such a cutoff height for vegetation.

Many of these studies also did not indicate how peripheral and central individuals were classified (Table 1: 'no formally stated definition given'). In this brief sampling of the literature, nine studies presenting some amount of data on marginal predation and drawing conclusions about the presence of differential risk did not report how the subgroups were defined, although many of these studies probably used a strict criterion to classify individuals, such as polygon vertices (e.g. Hoogland & Sherman 1976; P. W. Sherman, personal communication).

The fact that most studies do consistently find a significant marginal predation effect might suggest that these problems with methodology and terminology are not clouding the bigger picture (i.e. that marginal predation does exist). However, categorizing peripheral and central animals in an inappropriate way may be too artificial in some cases: 'peripheral versus central' may simply be two extremes of a continuum and contribute to a misunderstanding of the true risk dynamic within the group. One way to measure the gradient of risk accurately to the centre from the periphery of the colony is to measure risk as a continuous variable. Kruuk (1964) placed black-headed gull, *Larus ridibundus*, eggs in lines running from outside of the colony into the centre of the colony and measured egg predation. Predators generally stole eggs from outside the colony first, those from the edge of the colony next, and those from the centre last. This is a good way of measuring relative risk because it does not erroneously label individuals as peripheral or central and reveals the gradient of risk, whether it is linear, sigmoidal, or truly dichotomous (i.e. whether there is a distinct line of demarcation between centre and periphery). Continuous definition schemes are not methodologically possible for many types of animal groups (especially mobile herds or flocks), because the frequency of witnessing a predation event is typically low, and it is difficult to control a group of live animals, but they are probably possible for most colonial nesting species where egg predation is under consideration. When continuous data are not possible for colonial nesters, concentric circles (with the outer ring defined as peripheral and the inner circle as central) is a good option if an overhead map of the colony is available and the colony is not oddly shaped, because this also reduces the risk of misclassification of individuals.

Most investigators of mobile prey are forced to use a more dichotomous classification scheme that places individuals into distinct groups. In these cases, I propose using a definition that includes the best qualities of both the polygon vertices and layers of protection definitions. A 'maximum disparity' definition could define peripheral animals using the polygon vertices definition and define central animals using the layers of protection definition. Under this scheme, there would be greater assurance that individuals are accurately classified. If this maximum disparity scheme is not methodologically feasible, then the layers of protection definition is the next best option, because it is relatively permissive, statistically conservative and easy to use (one exception: for lekking species, thickness and degree of grass trampling is an accepted and effective definition of peripheral/central).

Clearly, there are many ways to define the term 'peripheral' or 'central'. Although most studies have found that central positions are safer than peripheral positions, the extreme variation in definitions used reduces the reliability of these conclusions. By choosing a definition that is either too strict or too permissive, we run the risk of rejecting marginal predation when differential risk actually exists. Using a continuous measurement of risk is the optimal methodology for immobile colonial nesters, but it is not realistic for many species.

The recommendation here for future studies of marginal predation is to use a maximum disparity definition that provides greater confidence that individuals are accurately classified. The problem of classification of location extends beyond the borders of the group. There is also variation in how studies measuring differences in predation rates between solitary individuals and grouped individuals define 'isolated' versus 'grouped' individuals. Thus, depending on the spatial distribution of the group, an individual classified as 'central' in one definition, might be classified as 'out of the group' in another.

### Defining Group Membership

Many studies on differential predation have measured the differences in risk between grouped individuals and isolated or solitary individuals. As was the case with intragroup marginal predation, there have been many suggestions for how to make the distinction between 'in the group' and 'out of the group'. Table 2 outlines some examples of common group membership criteria and sample papers that use each of them. The two most common ways to define group membership are distance-based: (1) the number of body lengths away from the nearest neighbour, or (2) some other criterion of absolute distance away from the group edge. All studies that reached conclusions about relative predation risk found that lone/stray individuals are more likely to be preyed upon than are other group members.

In a laboratory environment, biologists have found it easy to measure fish body length, and are able to quantify how many body lengths an individual is away from the rest of the school (Table 2). For example, Morgan & Godin (1985, page 238) defined 'straggling' killifish, *Fundulus diaphanous*, as 'individuals five body lengths (BL) or more from the nearest conspecific at the instant that an attack was initiated'. Their criterion was based on a mean nearest-neighbour distance within fish schools of less than three body lengths (Partridge et al. 1980; Pitcher & Wyche 1983). Parrish (1989) also conformed to this rule when defining stragglers in her study of Atlantic silversides, *Medina medina*, and Parrish et al. (1989) chose to use a five-body-length rule for their observations of flat-iron herring, *Harengula thrissina*. In this instance, a body of literature on one taxa seems to have come to a consensus on a biologically relevant criterion for determining group membership, which allows comparisons of predation rates between species.

Field biologists studying nesting colonies of birds or fish or mammalian herds have found it useful to define group membership by some absolute distance criteria (Table 2). Fitzgibbon (1990) defined individual Thomson's gazelles, *Gazella thomsoni*, as group members if they were within 50 m of each other. Colagross & Cockburn (1993, page 326) used a 30-m distance criterion for their observations on grey kangaroos, *Macropus giganteus*, but added the caveat that group members must have 'had the ability to communicate visually with the majority of other group members'. They remarked that, while other studies used a distance of 50 m, interactions at distances greater than 30 m were rare, and 'individuals

**Table 2.** Different ways 'in the group' and 'out of the group' have been defined in the literature and examples of studies where differences in predation risk between groups and solitary individuals were measured

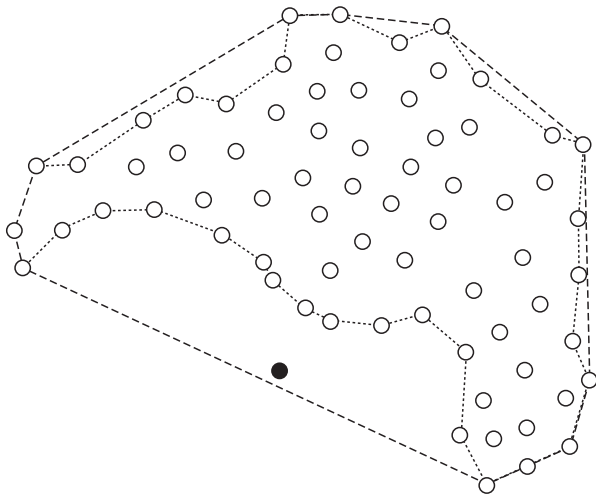
Technique	Reference	Species	Group type	Relative predation risk
Distance from group Body lengths	Morgan & Godin 1985	Banded killfish, <i>Fundulus diaphanous</i>	Fish school	Stray>Group
	Parrish 1989	Atlantic silversides, <i>Menidia menidia</i>	Fish school	Stray>Group
	Parrish et al. 1989	Flat-iron herring, <i>Harengula thrissina</i>	Fish school	Stray>Group
Absolute distance	Fitzgibbon 1990	Thomson's gazelles, <i>Gazella thomsoni</i>	Mammal herd	Stray>Group
	Colagross & Cockburn 1993	Grey kangaroo, <i>Macropus giganteus</i>	Mammal herd	No conclusion
	Gross & MacMillan 1981	Bluegill sunfish, <i>Lepomis macrochirus</i>	Nesting colony	Lone>Group
	Andersson & Wiklund 1978	Fieldfares, <i>Turdus pilaris</i>	Nesting colony	Lone>Group
	Tenaza 1971	Adélie penguins, <i>Pygoscelis adeliae</i>	Nesting colony	Lone>Group
Shadow intensity on bottom of tank	Jakobsen & Johnsen 1988	Water flea, <i>Bosmina longispina</i>	Insect swarm	Stray>Group
Number of 'neighbouring' nests	Dominey 1981	Bluegill sunfish, <i>Lepomis macrochirus</i>	Nesting colony	Lone>Group
No formally stated definition given	Taylor 1962	Adélie penguins, <i>Pygoscelis adeliae</i>	Nesting colony	Lone>Group
	Kruuk 1964 Patterson 1965	Black-headed gull, <i>Larus ridibundus</i>	Nesting colony	Lone>Group Lone>Group

separated by longer distances moved independent of the closest group' (page 326). Obviously, different species require a different absolute distance criterion based on their spatial distribution. Gross & MacMillan (1981, page 165) defined solitary male bluegill sunfish, *Lepomis macrochirus*, as having nests 1.5 m from other nests and they noted that this distance was sufficient for 'behavioural and probably visual isolation'. Andersson & Wiklund (1978) observed that fieldfare, *Turdus pilaris*, nests more than 75 m from their nearest neighbour gained little benefit of communal defence. Clutton-Brock et al. (1982), who termed red deer, *Cervus elaphus*, aggregations 'parties', used a nearest-neighbour criterion to define party membership. Examining the distribution of distances between all dyads in a population resulted in a bimodal distribution, with an appropriate distance criterion falling at the central minimum. To check this, Clutton-Brock et al. (1982) suggested measuring the activity synchrony of the parties, because the degree of synchrony within parties should be greater than that between parties. Although this method may work for distinguishing one 'party' from another, it does not help to establish whether an individual is in a group or isolated from the group, and it is also very difficult to perform in the field (but see Hoogland & Sherman 1976).

Although other studies have implemented unique methods for distinguishing between 'within the group' and 'out of the group' (e.g. Dominey 1981; Jakobsen & Johnsen 1988), most use some type of distance criteria to classify individuals. However, sometimes the in-out distinction is not so clear-cut. For example, Tenaza (1971) applied the following classifications to examine

predation in Adélie penguin, *Pygoscelis adeliae*, colonies: 'isolated' nests were located at least 2 m from their nearest neighbour and were outside of the colony, 'central' nests were surrounded by six other nests with no space to support additional nests, and 'peripheral' nests were located on the colony perimeter. He also provided photographs depicting examples of each nest classification. Figure 3 is a schematic representation of one 'fictional' Adélie penguin colony. According to Tenaza's definitions, which were clearly stated and legitimate for the study system, the black individual in Fig. 3 would be classified as isolated, with individuals lying on the dotted line considered peripheral (35 total). However, problems arise if we impose other definitions on the same fictional colony. If individuals were classified as peripheral or central according to polygon vertices, the black dashed line would be drawn around the entire colony with 11 individuals being classified as 'peripheral'. The black individual, classified as 'isolated' by Tenaza, lies inside this border of peripheral individuals, and would be classified not only as 'within the group' but as a 'central' individual.

Studies of differential predation risk should attempt to answer the underlying question: 'which spatial positions in a group benefit from the presence of nearby neighbours?' This question is often ignored either by excluding individuals obviously benefiting from group presence (Fig. 3) or including individuals that are clearly separated from the rest of the group. Here, the problem of relative size of the landscape arises. Deer 60 m from the herd may be classified as 'out of the herd' if they are in a small valley, but 'in the herd' if they are in the middle of an



**Figure 3.** Example of a fictional Adélie penguin colony. Following Tenaza (1971), the black individual is denoted as 'isolated' and the fine dotted line denotes the colony perimeter where 'peripheral' individuals are located. The heavy dashed line denotes the colony perimeter according to polygon vertices.

enormous expanse of grassland. The key issue is how much protection each individual is receiving from the herd. Habitat and landscape have an effect on predation risk and subsequent antipredator strategies, however, unless it is an extreme case where the herd is up against a cliff or next to a lake and the habitat is clearly protecting one side of the group, the results should be the same: given the same spatial configuration and the same predator, the individual predation risks should be the same in each scenario (small valley versus large grassland). It follows that, if we are to have objective operational definitions, the focal individual should receive the same classification in both scenarios. Although a preference for an absolute-length criterion appears to be the consensus in the literature, there must be some room for caveats and rules for exclusion/inclusion of borderline individuals (e.g. Colagross & Cockburn 1993). There are frequently behavioural differences between group members and strays: outliers tend to behave as though they are not part of the group. Being within sight of the group and not obstructed by trees or other physical boundaries is also an important criterion for membership in most groups. These rules are intended to address the most important criterion for group membership: benefit of protection by the presence of nearby neighbours.

### Importance of Predator Preferences

There are many costs and benefits to occupying different spatial positions in groups (reviewed in Krause & Ruxton 2002). By far the vast majority of studies measuring predation risk within animal groups have found that the risk of predation is greater on the periphery than in the centre (Table 1). However, for any study of differential risk, it is difficult to distinguish whether the predator

is focusing its efforts on peripheral individuals because they are the closest and most exposed, or because the peripheral individuals are of a certain phenotype (e.g. mostly males, smaller individuals, less dominant individuals, hungrier individuals, larger individuals). Most studies showing marginal predation do not (or cannot) control for other differences within the group or the biases that predators may have for attacking particular types of individuals. For example, are predators selecting edge individuals because they cannot penetrate the colony and because peripheral animals are, therefore, easier to catch regardless of any possible size, age, or rank differences? Or, do predators preferentially hunt a particular class of individuals because they are easier to capture and kill, and the individuals of this type located on the periphery of the colony are the only ones at risk? Although there is a great deal of empirical work on predator preferences for certain prey types (discussed in Krause & Ruxton 2002), there are only a few cited cases of predator preferences for particular prey types or regions within spatially heterogeneous animal groups (e.g. Walther 1969; Parrish 1989; Fitzgibbon 1990; Rayor & Uetz 1993; Brunton 1997).

Rayor & Uetz (1993, 2000) reported that risk of predation in the colonial web-building spider *Metepira incrassata* decreases with increasing distance from the colony edge, with position in the colony related to colony size and behavioural conflicts between individuals of differing size, rank and age. Large pompilid wasps, *Poecilopompilus mixtus*, which lay their eggs on individual *M. incrassata*, select from the few large spiders on the colony periphery, because larger hosts result in increased offspring fecundity (Rayor & Uetz 1993; Rayor 1997). Sphecid wasps (*Trypoxylon* sp.), which are much smaller than *P. mixtus* and cannot navigate within the web colony of *M. incrassata*, prey only on small spiders on the periphery. In this case, the nature of web spacing and the protective properties of silk webs as 'security alarms' based on web vibrations (Uetz et al. 2002) make these spider groups a special case of layers of protection. Taking a multiple-predator approach to studying animal groups shows the true breadth of possible selective agents that can affect the evolution and adaptiveness of gregariousness.

Fitzgibbon (1990) found that cheetahs, *Acinonyx jubatus*, attacked solitary female Thomson's gazelles more than solitary males; however, when attacking herds where males occupied more peripheral positions, they usually attacked males. These data indicate that cheetahs tend to hunt females first because they are easier to catch, but are relegated to hunting the more elusive peripheral males when hunting gazelle herds. Measuring how frequently different types of solitary individuals are killed can shed light on predation preferences in the absence of group protection. Walther (1969) showed that different species of predator have widely varying biases for different age and sex classes of gazelle, and therefore, we might also see intraspecific variation in predatory biases here as well. Walther observed seven different species of predators taking gazelles; although some did not discriminate on the basis of age or sex (cheetahs took both adult

and subadult males and females in herds), others focused on fawns (jackals, hyaenas, baboons). Therefore, we cannot extrapolate about relative predation risk on an entire prey species by looking at predation from only one predator species in the environment.

Studies that do not show marginal predation (e.g. Quinlan 1983; Parrish 1989) are the most informative about how predator–prey group systems operate. Parrish (1989) showed that black seabass, *Centropristis striata*, prey upon Atlantic silversides, *Menidia menidia*, using two distinctly different attack strategies. Although the seabass preferentially target the central individuals, the strategies differ in the manner in which the bass approach prey and the frequency and location of attack. Brunton (1997) found that central nests in least tern, *Sterna antillarum*, colonies have lower fledging success than do peripheral nests. Most nest predation is due to black-crowned night-herons, *Nycticorax nycticorax*, which only attack central nests, and less nest predation is due to American crows, *Corvus brachyrhynchos*, which only attack nests on the colony edge. These studies suggest that, in any animal group, the level of risk at any position will depend on which predator type is most common. For least terns, if the study had focused only on crow–tern predation events, the author would have concluded that peripheral nests were indeed at greater risk. This dependence on predator strategy will vary with the type of prey group and the other ways in which prey defend themselves. For instance, nesting colonies of sandwich terns show high levels of communal defence and mobbing behaviour (Veen 1977). It may not be possible for an aerial predator to attack from above due to the terns' antipredator aggression; thus, the only possible mode of attack is to approach the colony from the side and attack peripheral nests, which enjoy less protection from neighbours.

Finally, if individual characteristics influence which animals within a group are attacked or preyed upon, then models of grouping behaviour that assume predators attack the nearest individual will be inaccurate. In one of the first models attempting to explain grouping, Vine (1971) assumed that a predator would take the nearest prey. Although Vine's model does predict the formation of aggregations in cases where the predator approaches from outside the group of prey, something which Hamilton's (1971) model does not do, it cannot apply to systems where predators make deliberate decisions about which prey to attack based on some trait preference. Here, the crucial assumption of attacking the nearest prey individual is violated, and other predator-based assumptions (e.g. preferences for particular prey types, varying attack strategies, etc.) must be used to explain animal aggregations.

## Summary

The problems that exist in the measurement of marginal predation clearly extend beyond simple terminology. Predators often have preferences or biases for particular prey types, and individual characteristics of prey may also affect which individuals are most

frequently attacked. In most predator–prey interactions, individuals on the periphery of a group are more at risk of predation than those in the centre, and outliers are at even greater risk. But classification techniques have varied widely and many of the accepted definitions are prone to errors in classification. Although universal definitions of 'centre', 'periphery' and 'outlier' may not be feasible due to the variation in types of spatial distributions within animal aggregations, I make several recommendations regarding the selection of definitions for different group types: (1) in immobile colonial nesting species, a continuous measurement of predation from peripheral to central captures the true gradation of risk; (2) in mobile animal groups, the maximum disparity scheme, a combination of polygon vertices and layers of protection, can minimize misclassification of central and peripheral individuals; and (3) although an absolute-distance criterion is widely accepted for classifying solitary versus grouped individuals, behavioural differences between individuals should also be considered when making these classification decisions. Finally, before making sweeping conclusions about differential risk in a particular species, we should pay more attention to all possible sources of predation and not focus solely on one predator species. The key issues for future marginal predation studies are that the definitions used in practice should consider the relative protective benefit each individual receives from group living by evaluating risk from multiple predators and determining what factors might bias the predator's selection of individuals (typically peripheral) within the group.

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