Optimal individual positions within animal groups

Lesley J. Morrell\textsuperscript{1} and William L. Romey\textsuperscript{2}

\textsuperscript{1}Institute of Integrative and Comparative Biology, Faculty of Biological Sciences, University of Leeds

\textsuperscript{2}Department of Biology, State University of New York at Potsdam

Correspondence:
Lesley J. Morrell
Institute of Integrative and Comparative Biology
LC Miall Building
University of Leeds
Leeds
LS2 9JT
UK

Tel: +44 (0) 113 343 7377
Email: L.J. Morrell@leeds.ac.uk
Abstract

Animal groups are highly variable in their spatial structure, and individual fitness is strongly associated with the spatial position of an animal within a group. Predation risk and food gains are often higher at the group peripheries; thus, animals must trade off predation costs and foraging benefits when choosing a position. Assuming this is the case, we firstly use simulation models to demonstrate how predation risk and food gains differ for different positions within a group. Secondly, we use the patterns from the simulation to develop a novel model of the trade-off between the costs and benefits of occupying different positions, and predict the optimal location for an animal in a group. A variety of testable patterns emerge. As expected, increasing levels of satiation and vulnerability to predators, and increasing predation risk result in increased preferences for central positions, likely to lead to increased competition or more tightly packed groups. As food availability increases, individuals should first prefer center positions, then edge, returning to central positions under highest food levels. Increasing group size and/or density lead to more uniform preferences across individuals. Finally, we predict some situations where individuals differing in satiation and vulnerability prefer a range of different locations, and other situations where there is an abrupt dichotomy between central and edge positions, dependent on the levels of monopolization of food by peripheral individuals. We discuss the implications of our findings for the structure of groups and the levels of competition within them, and make suggestions for empirical tests.

Keywords: group living, optimization, simulation model, group structure, competition.
Introduction

There is growing evidence that the costs and benefits of group living are not experienced equally by all members of the group. The spatial structure of groups is highly variable (Parrish and Hamner 1997; Krause and Ruxton 2002), and evidence suggests that fitness is strongly related to the spatial position of an individual within a group (Krause and Ruxton 2002). In mating groups (e.g. leks), positional preferences for individuals are well understood (Fiske et al. 1998), and thus we consider here only non-mating groups. Energy intake, energy expenditure and predation risk are likely to be the major factors which differ with respect to position within a stationary group.

The theory of marginal predation (Hamilton 1971; Vine 1971) suggests that if predators always attack the nearest prey, then peripheral individuals should experience greater risk, and there is good evidence to suggest that this is the case. Across taxa, the levels of predation experienced by animal in a group increases with the distance from the centre (e.g. lapwings Vanellus vanellus; Šálek and Šmilauer 2002), spiders Metepeira incrassata (Rayor and Uetz 1990), mussels Mytilus edulis (Okamura 1986), and see (Stankowich 2003) for a review). Even when predators have equal access to central and peripheral individuals, predators still select marginal prey (Romey et al. 2008), and sensory biases for peripheral individuals on the part of their predators could contribute to these preferences (Tosh et al. 2006). Using simulation models, Bumann et al. (1997) demonstrated that predation risk may be strongly biased towards peripheral positions in large shoals of fish.

Foraging gains are also likely to be higher on the periphery of groups foraging on dispersed food particles, as the capture of food items by peripheral individuals limits
the food resources available to those in the centre (Wilson 1974). Burrowing spiders
(Seothyra henscheli) show increased growth rates when they are positioned at the
edge of a group (Lubin et al. 2001). Similar benefits to peripheral positioning have
been demonstrated in some colonial spiders Metepeira incrassata (Rayor and Uetz
1990, 1993). Antlion larvae (Myrmeleon immaculatus) relocate their pits to the
periphery of groups, forming groups in the shape of hollow circles, to minimize this
competition (Linton et al. 1991). In fish, individuals at the front of moving shoals are
more likely to obtain food (Krause 1994), and in groups of whirligig beetles (Dineutes
spp.) 95% of food particles are captured by the outer echelon of individuals (Romey
1995). Simulation modeling illustrates that such competition increases in intensity as
the density of a group increases. In high density groups, only peripheral individuals
can forage successfully, but in low density groups, some prey items reach the group
centre (Lubin et al. 2001).

To maximize survival, individuals within a group need to simultaneously avoid
starvation by foraging, and avoid falling prey to a predator. The experimental and
theoretical evidence above demonstrates that both tend to be significantly higher at
the periphery of a group, and thus an individual cannot simultaneously choose one
position that maximizes both. Gregarious animals have been shown to balance these
competing selection pressures (Okamura 1986; Rayor and Uetz 1990), and base their
decisions both on external pressures, and on internal state variables such as hunger
levels (Krause 1994; Romey 1995). There are several mechanistic models which
relate proximate factors such as attraction-repulsion rules, speed and trajectory to
group position (Romey 1996; Krause et al. 2000; Hemelrijk and Kunz 2005), but few
that directly tie evolutionary fitness to position (but see Beauchamp (2007) for a
theoretical study of the effect of spatial position on vigilance and survival),
particularly when considering trade-offs between differing selection pressures.

Here, we investigate the effect of the trade-off between foraging gains and predation
risk on the optimal position for an individual within a group. There are several key
areas that we will examine: firstly, we will look at how internal state variables
influence position preferences. A fully satiated individual, for example, might be
predicted to occupy a central position where it is safer from marginal predation, but
how would intermediately satiated individuals trade off the foraging gains and
predation risk of peripheral positions? Secondly, we will investigate how external
selection pressures such as food availability and predation risk affect an individuals’
position preference. Finally, we will study the impact of group properties (such as size
and density) on optimal positions. Our aim is to generate the first general predictions
regarding the spatial positioning of individuals, as a function of empirically
manipulable conditions, and to investigate possible implications for group structure
and competition levels within the group.

Our model is applicable to groups in which social hierarchies have not developed.
There are several terms in the literature that are used to describe this type of simple
group, including ‘congregation’ (Parrish and Hamner 1997), ‘ephemeral group’
(Hirsch 2007) and ‘FSH’ (for flocks, shoals/schools and herds; Romey 1997). The
primary criteria are that individuals do not form long lasting dominance hierarchies,
they are gregarious, and entry to or exit from the group is not restricted. Fish shoals
and insect swarms are good examples of this type of group. In more complex groups,
with, for example, stable dominance hierarchies, interactions between individuals are
partly responsible for determining positions within the group (Hirsch 2007). Examples of such groups include primates, foraging bird flocks and ungulates (Barta et al. 1997; Ruckstuhl and Neuhaus 2005; Hirsch 2007). However, at times, even these types of groups might act in the simple way we propose here (such as during times of migration when smaller groups combine into larger ones for several weeks of the year).

A Simple Conceptual Model

The evidence presented above suggests that both food availability and prey capture rates are greater on the edge than at the centre of a (stationary) group. Therefore, individuals occupying central positions should benefit from reduced predation risk, but pay the cost of reduced food intake. In contrast, peripheral individuals benefit from increased food intake, but suffer from greater levels of predation. It is also likely that the costs and benefits of occupying different spatial positions may be affected by the ‘state’ of the individual concerned. Hungry individuals may place a greater emphasis on foraging, and therefore be willing to accept a greater risk of predation, while individuals that are well-defended against predators (for example, those that have high levels of toxic compounds (Eisner 2003), strong behavioral defenses or large body size) may place a lower emphasis on risk.

In the conceptual model (figure 1), foraging success (probability of surviving) increases as individuals occupy more peripheral positions, and the probability of surviving a predator attack decreases as a function of risk. Hypothetical fitness functions are shown for two levels of hunger (satiated individuals are more likely to survive, regardless of their position) and two levels of defense (well-defended
individuals also have a higher survival rate). Individuals attempt to maximize their survival through both foraging gains and avoiding predators. The optimum position for an individual to occupy is found where overall survival is highest, which can be found most simply by multiplying the two fitness functions. A key assumption is that animals simultaneously, rather than sequentially, balance conflicting selection pressures, as found in previous manipulative studies (Romey 1995). There are likely to be other situations where individuals switch positions conditionally in response to a predation threat, for example (see Hamilton 1971). Although this conceptual model illustrates one potential class of functions linking position to evolutionary fitness, it has not been empirically tested whether the relationship between these factors is directly proportional. We use simulation modeling (see below) to generate patterns that are potentially more likely to be found in empirical systems. We take the results of the simulation modeling to develop an optimality model of the trade-off between predation risk and foraging gains.

Optimality model of position trade-offs

1. Simulation of predation risk and foraging gains

Previous authors have modeled how predation risk and foraging gains change as a function of the distance from the centre of a group (Linton et al. 1991; Bumann et al. 1997; Lubin et al. 2001). We follow their approaches here to simulate how predation risk and foraging gains change with position in a group, and how risk and gains are affected by parameters of interest. Our aim is to build on this background to generate predictions for patterns of food gain and predation risk as a function of spatial position and other parameters of interest, in the same modeling environment, from which we can develop a specific model of this trade-off. All modeling was carried out
in Matlab R2006b. In the simulation, \( N \) point-like individuals are positioned within a circle of radius \( r \) (Figure 2). 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 centre of the circle. Distances \( (d) \) were selected as the square root of a distance picked from a uniform distribution between 0 and \( r^2 \). This approach gives a uniform density of points within a circle. We carry out separate simulations for predation risk and foraging gains as these are measured in different ‘currencies’ (per capita predation risk and per capita number of food items consumed, see below), which are difficult to combine into a single fitness measure (Krebs and Kacelnik 1991; Clark and Mangel 2000). Risk and gains are combined in the optimality model below.

**Predation risk**

\( P \) predators were added within a circle of radius \( R \) (figure 2a), using the same methodology as for the prey. We use a large value of \( R \) (\( R=20 \)) such that the vast majority of predators predominantly appear outside the prey group, attacking from the periphery (Hamilton 1971), although some predators may attack from inside the group, particularly when \( r \) is larger (\( r = 10 \) is the largest value we use: 25% of predators attack from within the group in this case). Although marginal predation is common, one can imagine some situations where central individuals may be attacked: ground or water-surface dwelling animals subject to aerial predation for example. (Parrish 1989) found that fast moving predatory fish are able to capture prey in the centre of the shoal. Prey individuals are attacked solely based on their position (Ranta et al. 1994); each predator attacks the nearest prey individual (Hamilton 1971; Bumann et al 1994), with a probability \( a \) that the prey avoids the predator attack. Prey
avoidance probability \( a \) therefore measures the level of anti-predator defense possessed by the prey. This may be in the form of physical defenses such as spines or distasteful chemicals, or in the form of behavioral defenses such as a rapid escape response, or vigilance allowing the prey to detect the predator and then escape. We record the distance from centre \((d)\) for each successfully attacked prey individual. Each predator attacks in turn, and consumed prey are removed from the group. We are interested in how animals should respond to overall levels of predation risk rather than immediate behavioral responses to the presence of an attacking predator. We therefore assume no collective vigilance by the prey group, which may result, for example, in the rapid compaction of a prey group when a predator appears (e.g. (Foster and Treherne 1981; Krause and Tegeder 1994). Such behavioral responses to an attacking predator have been studied in the context of selfish herd behavior, for example ((Hamilton 1971; Morton et al. 1994; Viscido et al. 2002; Morrell and James 2008).

We divided the group into 20 concentric zones, of equal width. Thus, the edge of the most central zone was located a distance \(r/20\) from the circle centre, and contained all individuals in that area, and the most peripheral zone contained those individuals between \(0.95r\) and \(r\) from the centre. Thus, more individuals were able to occupy peripheral positions than central ones. The per capita risk for each zone was calculated as the number of attacks directed at individuals in that zone, divided by the total number of individuals in the zone. Figures 3 and 4 are plotted as per capital risk against the lower bound of each zone (i.e. the risk for individuals in the most central zone are plotted against zero, and for those in the most peripheral zone, risk is plotted against 0.95). We ran 10000 simulations for each set of parameter values to obtain an
estimate of the mean per capita predation risk for each zone. Each simulation consisted on one attack by each of the $P$ predators.

Food gains

A fixed number of food items $f$ enter the prey circle sequentially (Figure 2b). Individuals intercept food items moving in straight lines across the circle, and are equally likely to appear at any point outside the group. Food items are modeled as chords drawn within the group circle. Following Baker & Zemel (2000) we use an unbiased algorithm for the identification of chords, thus, the probability of a chord crossing over any given point within the circle is independent of the position in the circle (Baker and Zemel 2000). First, we randomly select an angle $\alpha_f$ from the circle centre, and then a distance from the centre $d_f$ (from a uniform distribution between 0 and $r$). The chord is then drawn at right angles to $\alpha_f$, passing through the position defined by $\alpha_f$ and $d_f$. A food item moves along the length of the chord in discrete steps, and at each step we calculate the distance from each prey individual to the food item. The first individual within a capture distance $c$ successfully consumes the food item. If no individuals are within the capture distance, the food item moves another step. If more than one individual is within $c$, then the closest is assumed to successfully consume prey. A large value of $c$ means that individuals can move some distance to intercept prey items (individuals in mobile groups such as whirligigs, for example). A small value for $c$ indicates that individuals are unable to move large distances (foragers with fixed positions such as antlions). The value of $c$ is always smaller than the value of $r$, constraining individuals to movement less than the radius of the group, but allowing movement outside the group boundary to intercept prey (similar to a fish darting out from a shoal to capture a prey item). There is no limit on
the number of prey items any individual can consume, and all prey items carry equal
nutritional value. After capturing a food item, individuals return to their original
location within the group. We calculate the total number of food items consumed by
each individual, and use this to calculate the per capita food consumption for
individuals in each zone (as above). Again, we ran 10000 simulations for each set of
parameter values to obtain an estimate of the mean per capita foraging success for
individuals in each zone.

We use the simulation model to investigate the relationship between distance from
group centre and predation risk. We vary each parameter separately while holding the
others constant. Figures give examples of the type of results our model generates. We
vary the size of the group ($N$), the density of the group ($N/r$), the number of predators
($P$), the radius of the circle in which the predator appears (and therefore the
probability that the predator attack comes from outside the group; $R$) and the
probability that an individual avoids a predator attack ($a$). To investigate the
relationship between distance from group centre and foraging gains, we vary group
size ($N$), the number of food items ($f$), the capture distance ($c$), and the radius of the
group ($r$; this effectively alters the density, calculated as $N/\pi r^2$).

**Results of simulated foraging and predation**

In line with our expectations and the findings of previous simulations (Linton et al.
1991; Bumann et al. 1997), predation risk and foraging gains both increase with the
distance from the group centre (figures 3 and 4). Each panel in figures 2 and 3 shows
the per capita risk (figure 3) or per capita food gains (figure 4) for four different
values for one of the variable parameters. All other parameters are kept constant. As
group size ($N$, but not density, $N/\pi r^2$ remains constant as $N$ increases) increases, per
capita risk decreases for all individuals, and is reduced to zero for those in central
positions (figure 3a). Increasing the number of predation events ($P$) also has the
expected effect of increasing risk, particularly for individuals towards the edge of the
group (figure 3b). An increased probability of escaping from a predator attack ($a$)
decreases overall risk (figure 3c). Finally, there was little effect of increasing the
density of the group (decreasing $r$) on predation risk (figure 3d).

Per capita foraging gains also decreased as group size ($N$) increased (figure 4a), as
food items were split amongst more group members. As the number of food items ($f$)
increased, capture rate also increased, although this was primarily of benefit to
peripheral group members (figure 4b); that is, our model predicts a greater asymmetry
in this one selective factor as food level increases. Peripheral individuals are
increasingly able to monopolize resources when capture distances ($c$) are large, but
food is more evenly distributed among members when their movement is constrained
(small values of $c$; figure 4c). Finally, lower densities of individuals within the group
(increasing $r$) lead to a more even distribution of food (figure 4d).

2. Simulation of optimal position within a group

We use the shapes of the curves generated using the simulation model above to define
suitable mathematical functions linking the position of an individual within a group to
the risk of predation and the gains from foraging. This approach allows us to
investigate more closely the impact of varying parameter values on the optimal
position of an individual within a group. The equations were chosen to approximate
the shape of the curves generated by the simulation model, and were fitted by eye to
the general shape of the data. Variation in the parameter values results in changes similar to those demonstrated by the simulation model, and the constants in each equation serve to match the shape and magnitude of the resulting curve more closely to the simulation results.

The costs \( C \) of occupying any given position within a group (figure 3) can be described by a logistic function of the form:

\[
C = 2\left(\frac{P(1-a)}{N}\right)\left(\frac{1}{1+e^{-N(d-1)}}\right)
\]  

(1)

This value represents the probability that an individual is successfully attacked by a predator, given its position within the group and the number of predation events relative to the size of the group.

The number of food items an individual is able to obtain, given their position within the group (figure 4), can be described using a similar function:

\[
F = \frac{0.1f}{r} + \frac{f}{N}
\]  

(2)

The constants 0.1, 100 and 0.8 serve to approximate the shape and magnitude of foraging gains curve generated by the simulation model. An individual’s probability of surviving is a function of the number of food items gained, and their current level of satiation \( s \). A food item gained by an individual with a low satiation level decreases their probability of starvation by a greater amount than the same food item gained by an individual whose satiation level is already high. We calculate the
probability that an individual starves ($S$), given its current food reserves and the gains from occupying any position using the following equation:

$$S = \frac{2}{1 + e^{0.5(s+F)}}$$  \hspace{1cm} (3)

The fitness of an individual depends on it avoiding both predation and starvation, and this is a multiplicative function (as illustrated in figure 1) of the probability that it avoids starvation ($1-S$) and the probability that the individual avoids predation ($1-C$):

$$W = (1-S)(1-C)$$  \hspace{1cm} (4)

The optimal position of an individual within a group is given by the value of $d$ which maximizes the value of $W$.

We investigate the effect of altering the parameters on the optimal position of an individual in a group. In particular, we are interested in the effect of the internal state variables (escape probability $a$, satiation $s$) and environmental selection pressures (food availability $f$, predation risk, $P$) on optimal group position. We also investigate the effects of changes in capture distance ($c$), group radius ($r$) and group size ($N$).

**Results for optimality model**

Our model makes a number of predictions as to how the optimal position of an individual within a group varies according to the parameters of the model. We see a number of intuitive results (figure 5). Firstly, as satiation level increases, or probability of escaping from a predator decreases, animals preferentially occupy
central positions (figure 5a). This predicts that within a group of individuals where there is variation in satiation and defense levels, there should be considerable variation in optimal positions for those individuals. Central positions would be occupied by satiated individuals with little chance of escaping a predator, whereas peripheral positions would be occupied by hungry individuals with a good chance of escaping from a predator, as predicted by the simple conceptual model of figure 1.

Figure 5a represents baseline levels: figures 5b-d represent results when a single parameter value relative to figure 5a. Increasing the risk of predation (figure 5b) results in an increased preference for central positions (comparing figure 5a with 5b, which illustrates the effect of increasing predation risk) for any given combination of satiation and escape probability. This would predict that competition for central positions may increase, or groups may become increasingly compact, with reduced distances between individuals. Increasing group size (but not density; figure 5c) results in more uniform preferences: differences in satiation and defense levels have a lower impact on position preferences in larger groups than in smaller groups, for constant levels of food availability and predation risk (comparing figures 5a and 5c). In this case, we would predict that animals would be competing for similar positions within a group, however, preferences are for reasonably peripheral positions, and we may expect the group to expand. Finally, increasing the density of the group (but not the number of individuals; figure 5d) results in a shift in preference for more peripheral positions (comparing figures 5a and 5d), particularly for individuals with high satiation levels but low probabilities of escaping from a predator attack. High densities may therefore also lead to the group spreading out, and therefore becoming less dense.
The model also generates a number of less intuitive results, which suggest testable predictions not yet explored in empirical systems. For example, as food availability increases, preferences alter from central to peripheral positions (figure 6). Then, as food availability increases further, from intermediate to high levels, the optimal position shifts back to the centre again. This is likely to occur because low food availability means that the foraging gains from occupying peripheral positions are not sufficient to outweigh the predation costs of occupying those positions. As food availability increases, the potential benefits to be gained means that individuals can offset predation costs in peripheral positions. However further increases in food availability mean that more food items are able to penetrate into the centre of the group, and it becomes worthwhile for individuals to occupy those central positions once again. As the food available to a group increases, we might expect to see the group expanding and then contracting again as the optimal position preferences of individuals alter.

Figures 5 and 6 show a continuum of positional preferences, from centre to edge, including preferences for intermediate positions. Increasing the distance over which individuals can move to capture the prey \( (c) \) can result in a different pattern appearing. As capture distance increases, instead of a continuous set of preferences (figure 7a), the range of satiation and defense combinations which predict intermediate optimum positions decreases (figure 7b). Further increases in capture distance lead to preferences for either very central or very peripheral positions (figure 7c and d). When individuals can only move a short distance relative to the area of the group (low \( c \)), many food items will penetrate the group, meaning that central individuals benefit
from avoiding predation, but are also able to gain food. If individuals can move a 
greater distance relative to the area of the group, then individuals on the very edge of 
the group capture all the available prey items, leaving none for the central individuals. 
Satiated individuals (that do not need to capture food resources to ensure survival) 
therefore benefit by positioning themselves in a location which leads to the greatest 
avoidance of predation (the absolute centre of the group) while hungry and/or well-
defended individuals move to the position which affords them the greatest food 
capture (the very edge). In this instance we might expect to see a group with a very 
compact centre, but with reduced distances between neighbors.

Discussion

Our model illustrates a variety of potential optimum positions for individuals of 
differing internal state, namely satiation levels and escape capabilities. We focus our 
investigation on variations in patterns in these two internal factors, as these are the 
most likely to vary between individuals within a group. Factors such as the 
availability of food, the abundance of predators and the size of a group, for example, 
are likely to be common to all group members, and represent external selection 
pressures. If individuals within a group differ in satiation and escape capabilities, then 
our model demonstrates that they should differ in their positional preferences. We find 
conditions under which all individuals prefer similar locations within the group 
(figure 5c), conditions where there is a spectrum of preferences from central to edge 
positions (figure 5a), and conditions where there appears to be an abrupt 
dichotomy/cut-off in preferences for central and edge positions (figure 7). To our 
knowledge, this is the first time such patterns have been investigated theoretically,
and they have implications for the overall structuring of groups (Parrish and Edelstein-Keshet 1999).

If individuals show a spectrum of preferences based on their combination of satiation and escape parameters (figure 5a), then assuming relatively even variation in these parameters, each individual should be able to occupy its optimal position, and competition for positions within the group may be reduced. If, however, the majority of individuals show a preference for similar positions (figure 5c), we might expect that competition for those positions is increased. If overall preferences are for peripheral positions (figure 5c) then individuals are likely to move outwards, leading to an increase in the area occupied by the group, or the formation of circular groups with empty centers (Barta et al. 1997). Alternatively, such patterns may lead to the breakdown of the group, as individuals move further apart in order to maximize their foraging success. Outward movement of individuals is likely to be triggered by cues such as a reduction in perceived levels of predation risk, increased group size (if two groups merge, for example), or increasing hunger levels for an individual.

If all individuals prefer more central positions (as would happen if predation risk increased (figure 5b), or food availability was high (figure 6), or individuals became increasingly satiated) then groups should become increasingly compact. Increasing density of individuals within a group (i.e. increasing levels of aggregation) in response to a perceived predation threat is common across taxa (Foster and Treherne 1981; Krause and Tegeder 1994; Watt et al. 1997; Viscido and Wethey 2002). These predictions for changing group structure could easily be tested in empirical systems by, for example, altering the availability of food.
If all individuals have preferences for similar, central locations, they might also be predicted to compete for those preferred positions. In our model, we assumed the absence of interaction effects between individuals which might lead to competition and dominance hierarchies (despotic distributions). In groups where membership is constant and individual recognition is possible, such hierarchies often develop (see Hirsch (2007) for a review). In such groups, individuals are unlikely to be free to position themselves at their optimum point, as there is likely to be competition for positions within a group. Dominance, for example, is known to structure groups, with dominant individuals occupying central positions and forcing subordinates to the periphery (e.g. capuchin monkeys *Cebus capucinus* (Hall and Fedigan 1997)). However, our model may be useful in determining the types of environmental conditions under which competition for positions may arise. Where predation risk is high, for example, many individuals will have similar preferences for central positions, leading to high competition and potential for the development of hierarchies. Where there is a range of preferences for the individuals, competition for particular positions is less likely. Further modeling work could be used here to predict how groups are structured when individuals are not free to occupy their optimal position, but must contend with conspecifics who may be seeking similar positions.

Even in the absence of direct competition for positions, individuals within a group may impact on food intake and anti-predator behavior of others. Our model already includes the effects of shadow competition (Wilson 1974), where peripheral individuals limit the availability of food to central ones, but the position occupied by any given individual is likely to depend on the behavior of the other group members.
If the majority of individuals moved to peripheral positions, for example, an isolated individual in the center of a group may be at greater predation risk due to its isolation and might benefit by moving towards other individuals (Hamilton, 1971), away from the center of the group. A game theoretical approach where individual decisions are influenced by the choices of other group members (Houston et al. 2003; Morrell 2004; Morrell and Kokko 2004) would provide a more accurate picture of the dynamics of spatial positioning within groups, and allow investigation of how competition for positions within groups could be played out. Our model does not include this level of complexity, but provides a basis upon which such a game theory model could be built, and provides predictions that could be tested in empirical systems.

A final pattern that we observe from our model is one where either very central or very peripheral positions are preferred (figure 7c-d). It is more difficult to predict the structure of the group from this pattern, although we may expect to see groups remaining together, with a cluster of individuals at the centre and others occupying the periphery. In whirligig groups, for example, central individuals tend to be closely packed, and nearest-neighbor distances increase towards the periphery of the group (Romey 1995). Alternatively, as mentioned above, the positioning of other individuals in the group may exert a strong influence on the behavior of others, causing central individuals to move to more peripheral positions (to benefit from the dilution effect (Foster and Treherne 1981), for example), or peripheral individuals moving into a second ‘tier’ behind the most peripheral to reduce their predation risk (Hamilton 1971). Moving away from other individuals may also lead to a perceived reduction in group size, altering the trade-off and changing the optimal location for an individual.
Empirical investigation or more complex modeling approaches could shed light on how animals respond to conditions such as these.

The majority of studies looking at the effect of group positioning consider only ‘central’ versus ‘peripheral’ individuals, with no intermediate individuals – they are either on the edge or not. Thus, there is a lack of empirical data defining the shapes of the foraging and predation risk curves. However, some empirical studies suggest that predators attack only the most peripheral individuals in a group. In fish attacking Daphnia (Milinski 1977) or groups of surface-dwelling whirligigs (Romey et al. 2008), the predators choose only the individuals on the very edge, suggesting intermediate positions are actually as safe as those in the very centre. Empirical work is needed to investigate this, as our results are likely depend on the shapes of the curves that are assumed to link distance from the group centre with predation risk and food availability or intake. However, under certain parameter values, our model in fact predicts a dichotomy between individuals that prefer central positions and those that prefer edge positions. Only small alterations in their levels of satiation or escape probability switch preferences from the centre to the edge, suggesting that categorizing individuals as central or peripheral may be an adequate description.

Our model includes several further simplifying assumptions. Firstly, the selection pressures that we considered most important to the fitness of individuals within a group were predation and food distribution, but there are other factors which could influence fitness and should be considered in future studies (such as energy expenditure or potential for reproduction). We assume that there are foraging benefits to occupying peripheral positions – our model applies to situations where groups are
foraging on dispersed food resources. Alternatively, groups may be centered on a food resource or moving together towards aggregated resources. If this is the case, then food gains are likely to be higher for centrally positioned individuals, or those leading the groups. In this case, dominance will play a key role in the structuring of the group, as dominants are able to monopolize access to food (Hirsch 2007), and simultaneously occupy lower predation risk positions.

Our model considers only stationary groups, but in many species, moving groups are common. Rather than differential predation risk and foraging gains from centre to edge, these groups are likely to differ from front to back. Individuals at the front of moving groups tend to have higher foraging success, and front positions tend to be occupied by hungry individuals (Krause et al. 1998; Romey and Galbraith 2008). There is, however, likely to be an energy cost in occupying front positions, and individuals at the back can make considerable energetic savings (Krause and Ruxton 2002). Predation risk is also likely to vary as a function of distance from the front of a group. In chub (Semilotus atromaculatus), individuals occupying front positions suffered from greater levels of predation than individuals in rear positions (Bumann et al. 1997). Front positions may therefore be equivalent to edge positions, but with the added energetic costs.

Predators may also make deliberate decisions as to which individual within a group prey to target, rather than attacking peripheral individuals at random (Stankowich 2003). Predators may more successfully track individuals at the edge of groups due to the confusion effect (Neill and Cullen 1974), explaining why in some systems only very peripheral individuals are attacked (Romey et al. 2008; Milinski 1977).
Alternatively, predators may attack individuals that are phenotypically or behaviorally distinct from the rest of the group (the oddity effect; (Landeau and Terborgh 1986). Sparrowhawk (*Accipiter nisus*) attacks on redshank (*Tringa totanus*) depend on several behavioral factors related to the vulnerability of the prey (Quinn and Cresswell 2004), rather than solely on position within the group. Isolation of individuals may also be important: the selfish herd hypothesis predicts that individuals are attacked in proportion to the size of their ‘domain of danger’, the area around each individual that is closer to it than to any other individual (Hamilton 1971). The perceptual ability of a predator may also limit predation risk for peripheral foragers (James et al. 2004; Morrell and James 2008). Levels of anti-predator vigilance may also play a role, and may differ spatially within groups (Beauchamp 2007). Higher vigilance by peripheral individuals may reduce the foraging benefits associated with occupying such positions, for example, leading to increased preferences for central locations, or occupation of peripheral positions by more satiated individuals who have less need to forage.

Individuals are likely to want to switch positions within a group. In colonial spiders (*Metepeira incrassata*), larger females with egg sacs show a strong preference for central positions, while younger spiders prefer peripheral positions, as they have yet to attain sufficient size for successful reproduction (Rayor and Uetz 1993). If hungry individuals occupy peripheral positions, then as those individuals become increasingly satiated, their preference for the safer, central locations should increase, resulting in a rotation of positions within a group (see also (Krause and Ruxton 2002). Such a cycling of positions due to changing hunger levels can be seen in whirligig groups (Romey 1995). Nutritionally deprived roach (*Rutilus rutilus*) and chub (*Leuciscus*...
cephalus) show strong preference for front positions (Krause 1993a), but frightened
minnows (Phoxinus phoxinus) tended to seek positions in the centre of shoals (Krause
1993b, c).

We included satiation and the ability to escape once attacked as the internal state
variables in our model. In reality, both of these factors may be correlated with an
individuals size, parasite load, age (Krause and Ruxton 2002) and sex (Romey and
Wallace 2007), or may be dependent upon one another, if an animal’s ability to
escape from a predator depends on its energy levels, or investment in chemical
defenses (i.e. condition dependent anti-predator responses). These patterns may either
confound attempts to distinguish the factors underlying positional choices, or provide
a means by which preferences can be systematically investigated. In the laboratory,
many of the parameters of our model (such as hunger levels, food availability and
perceived risk of predation) can easily be manipulated, and in certain species, this
may also be possible with levels of defense. It would be instructive to investigate
levels of competition and group structure in response to changes in these parameters,
for groups where individuals differ in one or more of the internal state variables.

Combining different factors such as foraging and predation risk into a single fitness
function can also be problematic, as they are measured in different currencies (one as
a risk and one as food intake). Stochastic dynamic modeling provides useful
methodology for combining currencies that can be measured in natural systems
(Krebs and Kacelnik 1991; Clark and Mangel 2000; Krause and Ruxton 2002), and
this approach could be applied to the positioning behavior of individuals within
groups (Krause and Ruxton 2002; Hirsch 2007). Finally, there are many other factors
which may influence positioning within a group and which should be considered in future approaches, including dominance hierarchies (Hirsch 2007), aggression (Hemelrijk 2000), food acquisition tactics (producer-scrounger behavior; (Barta et al. 1997; Mónus and Barta 2008), condition-dependent predator avoidance, trade-offs with other behaviors such as vigilance or mating (Houston et al. 2003; Morrell 2004; Jackson and Ruxton 2006) and game theoretical approaches. Such future investigations could provide a fascinating insight into the dynamics of grouping in animals, extending the predictions we make here.

Acknowledgements

We would like to thank Jens Krause, Colin Tosh, Anne Houde and 2 anonymous referees for useful comments on the manuscript. This work was funded by a NERC Postdoctoral Fellowship (NE/D008921/1) to LJM and NSF grant IBN-0315474 to WLR.

References


**Figure legends**

**Figure 1:** a) Conceptual model relating fitness to the distance from the centre of the group. Food availability and risk of predation increase with distance from centre, for individuals that are hungry or satiated and at low (defended) or high (vulnerable risk of predation). b) Graph of combined fitness due to multiplicative effects of a given combination of food availability and predation risk (e.g.: defended x hungry). Filled circles and dropped lines indicate the optimum distance from the centre for each type of individual.

**Figure 2:** $N$ individuals (black filled circles, here $N=10$) are placed within a circle of radius $r$ (solid edged circle). Each individual is a distance $d$ from the centre of the circle. a) Predators, $P$ (large checkerboard circle, here $P=2$) appear at random within a circle of radius $R$ (dashed circle) and attack the nearest individual (solid arrow). b) Each individual can move a distance $c$ to capture food items (dotted circles surrounding the individuals). Food items ($f$) enter from the outside of the group (dashed lines) and are intercepted by individuals at the solid diamond. Note that figures 2a and 2b are drawn to different scales.

**Figure 3:** Effect of varying parameters on the link between occupied position ($x$-axis) and per capita risk of predation ($y$ axis) in the simulation model. a) Varying group size ($N$). Filled squares: $N=10$, filled circles: $N=20$, open squares: $N=50$, open circles, $N=100$. b) Varying number of predators ($P$). Filled squares: $P=1$, filled circles: $P=2$, open squares: $P=5$, open circles, $P=10$. c) Varying the probability an individual evades a predator attack ($a$). Filled squares: $a=0$, filled circles: $a=0.2$, open squares: $a=0.4$, open circles, $a=0.6$. d) Varying the radius of the circle formed by the group ($r$):
equivalent to varying density). Filled squares: $r=1.128$, filled circles: $r=1.596$, open squares: $r=2.253$, open circles, $r=3.568$. For each panel, all other parameter values are: $N=20$, $P=2$, $a=0.2$, $r=1.595$. Distances from the centre are scaled between 0 and 1 (zero being the centre and 1 being the maximum value of $r$) to allow comparisons to be made between figure panels.

Figure 4: Effect of varying parameters on the number of food items captured in the simulation. a) Varying group size ($N$). Filled squares: $N=10$, filled circles: $N=20$, open squares: $N=50$, open circles, $N=100$. b) Varying number of food items ($f$). Filled squares: $f=10$, filled circles: $f=20$, open squares: $f=50$, open circles, $N=100$. c) Varying the distance over which an individual can capture a food item ($c$). Filled squares: $c=0.05$, filled circles: $c=0.1$, open squares: $c=0.2$, open circles, $c=0.3$. d) Varying the radius of the circle formed by the group ($r$: equivalent to varying density). Filled squares: $r=1$, filled circles: $r=2$, open squares: $r=5$, open circles, $r=10$. For each panel, all other parameter values are: $N=20$, $f=20$, $c=0.2$, $r=1.595$. Distances from the centre are scaled between 0 and 1 (zero being the centre and 1 being the maximum value of $r$) to allow comparisons to be made between figure panels.

Figure 5: Results of the model. a) The effect of increasing levels of satiation ($s$; x-axis) and probability of escaping a predator ($a$; y-axis). Shading indicates the optimal distance from the group centre of an individual with each combination of satiation ($s$) and escape probability ($a$), where black indicates central positions ($d=0$) and white indicates peripheral positions ($d=1$; all panels). Parameter values used: $N=10$, $P=2$, $f=20$, $c=0.05$, $r=2$. b) As panel a) but with predation risk increased to $P=5$. c) As panel
a), but with group size increased to \(N=20\). d) As panel a) but with group radius decreased to \(r=0.5\) (increased group density).

**Figure 6:** Effects of increasing satiation (\(s\)) and food availability (\(f\)) on the optimal distance from the group centre (\(d\)). Shading again indicates optimal position as in figure 4. Other parameter values used: \(N=10\), \(r=2\), \(a=0.2\), \(P=2\), \(c=0.05\).

**Figure 7:** Effect of altering capture distance (\(c\)) on optimal distance from the group centre (\(d\)). Each panel shows the effect of satiation (\(s\)) and escape probability (\(a\)) on optimal position in a group (\(d\)). Shading again indicates optimal position: black indicates centre positions (\(d = 0\)) and white indicates peripheral positions (\(d = 1\)). Each panel shows different value for capture distance (\(c\)). Other parameter values are \(N=10\), \(P=2\) and \(f=20\), \(r=2\). a) \(c=0.05\), b) \(c=0.075\), c) \(c=0.1\), d) \(c=0.15\).
Table 1: Parameters used in the models. Information in parentheses relates to the simulation model only.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Description</th>
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<tbody>
<tr>
<td>$N$</td>
<td>Number of individuals</td>
</tr>
<tr>
<td>$d$</td>
<td>Distance from the centre of the group</td>
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<tr>
<td>$r$</td>
<td>Radius of the circle in which the prey are positioned</td>
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<tr>
<td>$P$</td>
<td>Predation risk (number of predation events)</td>
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<tr>
<td>$R$</td>
<td>(Radius in which predators are positioned)</td>
</tr>
<tr>
<td>$a$</td>
<td>Probability that an individual avoids a predation attempt</td>
</tr>
<tr>
<td>$f$</td>
<td>Number of food items available</td>
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<td>$\alpha_f$</td>
<td>Angle used for calculating food trajectory</td>
</tr>
<tr>
<td>$d_f$</td>
<td>Distance used for calculating food trajectory</td>
</tr>
<tr>
<td>$c$</td>
<td>Distance individuals can move to capture the prey</td>
</tr>
<tr>
<td>$C$</td>
<td>Costs of occupying any given position within a group</td>
</tr>
<tr>
<td>$F$</td>
<td>Foraging gains from occupying any position within a group</td>
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<tr>
<td>$B$</td>
<td>Benefits of occupying any position within a group</td>
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<tr>
<td>$W$</td>
<td>Fitness of an individual</td>
</tr>
</tbody>
</table>
Figure 1
Figure 2

(a) Group size ($N$)

(b) Predators ($P$)

(c) Escape probability ($a$)

(d) Group radius ($r$)

Per capita predation risk vs. Lower bound of distance from centre

Predators ($P$) and the group radius ($r$) show an increase in risk as the lower bound of distance from the centre increases. Group size ($N$) and escape probability ($a$) also show an increase in risk, with escape probability showing a more significant increase. These patterns suggest that larger groups and better escape mechanisms are more effective in reducing predation risk.
Figure 3

(a) Group size (N)

(b) Food (f)

(c) Capture distance (c)

(d) Group radius (r)
Figure 4

(a) Probability of escaping from a predator (a) as a function of satiation (s) and optimal distance from the centre of the group (d).

(b) Same as (a) but with a different scale for optimal distance.

(c) Same as (a) but with a different scale for satiation.

(d) Same as (a) but with a different scale for optimal distance.
Figure 5
Figure 6