8 # Optimal individual positions within animal groups

9

10

11 Lesley J. Morrell[1] and William L. Romey[2]

12

13

14 [1]Institute of Integrative and Comparative Biology, Faculty of Biological Sciences,

15 University of Leeds

16

17 [2]Department of Biology, State University of New York at Potsdam

18

19

20 **Correspondence:**
21 Lesley J. Morrell
22 Institute of Integrative and Comparative Biology
23 LC Miall Building
24 University of Leeds
25 Leeds
26 LS2 9JT
27 UK
28

29 Tel: +44 (0) 113 343 7377

30 Email: L.J.Morrell@leeds.ac.uk

31

1   **Abstract**

2   Animal groups are highly variable in their spatial structure, and individual fitness is

3   strongly associated with the spatial position of an animal within a group. Predation

4   risk and food gains are often higher at the group peripheries; thus, animals must trade

5   off predation costs and foraging benefits when choosing a position. Assuming this is

6   the case, we firstly use simulation models to demonstrate how predation risk and food

7   gains differ for different positions within a group. Secondly, we use the patterns from

8   the simulation to develop a novel model of the trade-off between the costs and

9   benefits of occupying different positions, and predict the optimal location for an

10   animal in a group. A variety of testable patterns emerge. As expected, increasing

11   levels of satiation and vulnerability to predators, and increasing predation risk result

12   in increased preferences for central positions, likely to lead to increased competition

13   or more tightly packed groups. As food availability increases, individuals should first

14   prefer center positions, then edge, returning to central positions under highest food

15   levels. Increasing group size and/or density lead to more uniform preferences across

16   individuals. Finally, we predict some situations where individuals differing in

17   satiation and vulnerability prefer a range of different locations, and other situations

18   where there is an abrupt dichotomy between central and edge positions, dependent on

19   the levels of monopolization of food by peripheral individuals. We discuss the

20   implications of our findings for the structure of groups and the levels of competition

21   within them, and make suggestions for empirical tests.

22

23   **Keywords:** group living, optimization, simulation model, group structure,

24   competition.

25

26

1 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

3

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 has 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

1   theoretical study of the effect of spatial position on vigilance and survival),

2   particularly when considering trade-offs between differing selection pressures.

3

4   Here, we investigate the effect of the trade-off between foraging gains and predation

5   risk on the optimal position for an individual within a group. There are several key

6   areas that we will examine: firstly, we will look at how internal state variables

7   influence position preferences. A fully satiated individual, for example, might be

8   predicted to occupy a central position where it is safer from marginal predation, but

9   how would intermediately satiated individuals trade off the foraging gains and

10   predation risk of peripheral positions? Secondly, we will investigate how external

11   selection pressures such as food availability and predation risk affect an individuals'

12   position preference. Finally, we will study the impact of group properties (such as size

13   and density) on optimal positions. Our aim is to generate the first general predictions

14   regarding the spatial positioning of individuals, as a function of empirically

15   manipulable conditions, and to investigate possible implications for group structure

16   and competition levels within the group.

17

18   Our model is applicable to groups in which social hierarchies have not developed.

19   There are several terms in the literature that are used to describe this type of simple

20   group, including 'congregation' (Parrish and Hamner 1997), 'ephemeral group'

21   (Hirsch 2007) and 'FSH' (for flocks, shoals/schools and herds; Romey 1997). The

22   primary criteria are that individuals do not form long lasting dominance hierarchies,

23   they are gregarious, and entry to or exit from the group is not restricted. Fish shoals

24   and insect swarms are good examples of this type of group. In more complex groups,

25   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

6

1 individuals also have a higher survival rate). Individuals attempt to maximize their

2 survival through both foraging gains and avoiding predators. The optimum position

3 for an individual to occupy is found where overall survival is highest, which can

4 found most simply by multiplying the two fitness functions. A key assumption is that

5 animals simultaneously, rather than sequentially, balance conflicting selection

6 pressures, as found in previous manipulative studies (Romey 1995). There are likely

7 to be other situations where individuals switch positions conditionally in response to a

8 predation threat, for example (see Hamilton 1971). Although this conceptual model

9 illustrates one potential class of functions linking position to evolutionary fitness, it

10 has not been empirically tested whether the relationship between these factors is

11 directly proportional. We use simulation modeling (see below) to generate patterns

12 that are potentially more likely to be found in empirical systems. We take the results

13 of the simulation modeling to develop an optimality model of the trade-off between

14 predation risk and foraging gains.

15

16 **Optimality model of position trade-offs**

17 **1. Simulation of predation risk and foraging gains**

18 Previous authors have modeled how predation risk and foraging gains change as a

19 function of the distance from the centre of a group (Linton et al. 1991; Bumann et al.

20 1997; Lubin et al. 2001). We follow their approaches here to simulate how predation

21 risk and foraging gains change with position in a group, and how risk and gains are

22 affected by parameters of interest. Our aim is to build on this background to generate

23 predictions for patterns of food gain and predation risk as a function of spatial

24 position and other parameters of interest, in the same modeling environment, from

25 which we can develop a specific model of this trade-off. All modeling was carried out

1 in Matlab R2006b. In the simulation, N point-like individuals are positioned within a

2 circle of radius r (Figure 2). Individuals were placed at random by first selecting an

3 angle from a uniform distribution between 0 and 360°, and then a random distance

4 from the centre of the circle. Distances (d) were selected as the square root of a

5 distance picked from a uniform distribution between 0 and r^2. This approach gives a

6 uniform density of points within a circle. We carry out separate simulations for

7 predation risk and foraging gains as these are measured in different 'currencies' (per

8 capita predation risk and per capita number of food items consumed, see below),

9 which are difficult to combine into a single fitness measure (Krebs and Kacelnik

10 1991; Clark and Mangel 2000). Risk and gains are combined in the optimality model

11 below.

12

13 *Predation risk*

14 P predators were added within a circle of radius R (figure 2a), using the same

15 methodology as for the prey. We use a large value of R (R=20) such that the vast

16 majority of predators predominantly appear outside the prey group, attacking from the

17 periphery (Hamilton 1971), although some predators may attack from inside the

18 group, particularly when r is larger ($r = 10$ is the largest value we use: 25% of

19 predators attack from within the group in this case). Although marginal predation is

20 common, one can imagine some situations where central individuals may be attacked:

21 ground or water-surface dwelling animals subject to aerial predation for example.

22 (Parrish 1989) found that fast moving predatory fish are able to capture prey in the

23 centre of the shoal. Prey individuals are attacked solely based on their position (Ranta

24 et al. 1994); each predator attacks the nearest prey individual (Hamilton 1971;

25 Bumann et al 1994), with a probability a that the prey avoids the predator attack. Prey

1   avoidance probability *a* therefore measures the level of anti-predator defense

2   possessed by the prey. This may be in the form of physical defenses such as spines or

3   distasteful chemicals, or in the form of behavioral defenses such as a rapid escape

4   response, or vigilance allowing the prey to detect the predator and then escape. We

5   record the distance from centre (*d*) for each successfully attacked prey individual.

6   Each predator attacks in turn, and consumed prey are removed from the group. We are

7   interested in how animals should respond to overall levels of predation risk rather than

8   immediate behavioral responses to the presence of an attacking predator. We therefore

9   assume no collective vigilance by the prey group, which may result, for example, in

10   the rapid compaction of a prey group when a predator appears (e.g. (Foster and

11   Treherne 1981; Krause and Tegeder 1994). Such behavioral responses to an attacking

12   predator have been studied in the context of selfish herd behavior, for example

13   ((Hamilton 1971; Morton et al. 1994; Viscido et al. 2002; Morrell and James 2008).

14

15   We divided the group into 20 concentric zones, of equal width. Thus, the edge of the

16   most central zone was located a distance *r*/20 from the circle centre, and contained all

17   individuals in that area, and the most peripheral zone contained those individuals

18   between 0.95*r* and *r* from the centre. Thus, more individuals were able to occupy

19   peripheral positions than central ones. The per capita risk for each zone was

20   calculated as the number of attacks directed at individuals in that zone, divided by the

21   total number of individuals in the zone. Figures 3 and 4 are plotted as per capital risk

22   against the lower bound of each zone (i.e. the risk for individuals in the most central

23   zone are plotted against zero, and for those in the most peripheral zone, risk is plotted

24   against 0.95). We ran 10000 simulations for each set of parameter values to obtain an

1   estimate of the mean per capita predation risk for each zone. Each simulation

2   consisted on one attack by each of the P predators.

3

4   *Food gains*

5   A fixed number of food items f enter the prey circle sequentially (Figure 2b).

6   Individuals intercept food items moving in straight lines across the circle, and are

7   equally likely to appear at any point outside the group. Food items are modeled as

8   chords drawn within the group circle. Following Baker & Zemel (2000) we use an

9   unbiased algorithm for the identification of chords, thus, the probability of a chord

10   crossing over any given point within the circle is independent of the position in the

11   circle (Baker and Zemel 2000). First, we randomly select an angle α_f from the circle

12   centre, and then a distance from the centre d_f (from a uniform distribution between 0

13   and r). The chord is then drawn at right angles to α_f, passing through the position

14   defined by α_f and d_f. A food item moves along the length of the chord in discrete

15   steps, and at each step we calculate the distance from each prey individual to the food

16   item. The first individual within a capture distance c successfully consumes the food

17   item. If no individuals are within the capture distance, the food item moves another

18   step. If more than one individual is within c, then the closest is assumed to

19   successfully consume prey. A large value of c means that individuals can move some

20   distance to intercept prey items (individuals in mobile groups such as whirligigs, for

21   example). A small value for c indicates that individuals are unable to move large

22   distances (foragers with fixed positions such as antlions). The value of c is always

23   smaller than the value of r, constraining individuals to movement less than the radius

24   of the group, but allowing movement outside the group boundary to intercept prey

25   (similar to a fish darting out from a shoal to capture a prey item).   There is no limit on

1   the number of prey items any individual can consume, and all prey items carry equal

2   nutritional value. After capturing a food item, individuals return to their original

3   location within the group. We calculate the total number of food items consumed by

4   each individual, and use this to calculate the per capita food consumption for

5   individuals in each zone (as above). Again, we ran 10000 simulations for each set of

6   parameter values to obtain an estimate of the mean per capita foraging success for

7   individuals in each zone.

8

9   We use the simulation model to investigate the relationship between distance from

10 group centre and predation risk. We vary each parameter separately while holding the

11 others constant. Figures give examples of the type of results our model generates. We

12 vary the size of the group (N), the density of the group (N/r), the number of predators

13 (P), the radius of the circle in which the predator appears (and therefore the

14 probability that the predator attack comes from outside the group; R) and the

15 probability that an individual avoids a predator attack (a). To investigate the

16 relationship between distance from group centre and foraging gains, we vary group

17 size (N), the number of food items (f), the capture distance (c), and the radius of the

18 group (r; this effectively alters the density, calculated as $N/\pi r^2$).

19

20 **Results of simulated foraging and predation**

21 In line with our expectations and the findings of previous simulations (Linton et al.

22 1991; Bumann et al. 1997), predation risk and foraging gains both increase with the

23 distance from the group centre (figures 3 and 4). Each panel in figures 2 and 3 shows

24 the per capita risk (figure 3) or per capita food gains (figure 4) for four different

25 values for one of the variable parameters. All other parameters are kept constant. As

1   group size (N, but not density, $N/\pi r^2$ remains constant as N increases) increases, per

2   capita risk decreases for all individuals, and is reduced to zero for those in central

3   positions (figure 3a). Increasing the number of predation events (P) also has the

4   expected effect of increasing risk, particularly for individuals towards the edge of the

5   group (figure 3b). An increased probability of escaping from a predator attack (a)

6   decreases overall risk (figure 3c). Finally, there was little effect of increasing the

7   density of the group (decreasing r) on predation risk (figure 3d).

8

9   Per capita foraging gains also decreased as group size (N) increased (figure 4a), as

10   food items were split amongst more group members. As the number of food items (f)

11   increased, capture rate also increased, although this was primarily of benefit to

12   peripheral group members (figure 4b); that is, our model predicts a greater asymmetry

13   in this one selective factor as food level increases. Peripheral individuals are

14   increasingly able to monopolize resources when capture distances (c) are large, but

15   food is more evenly distributed among members when their movement is constrained

16   (small values of c; figure 4c). Finally, lower densities of individuals within the group

17   (increasing r) lead to a more even distribution of food (figure 4d).

18

19   **2. Simulation of optimal position within a group**

20   We use the shapes of the curves generated using the simulation model above to define

21   suitable mathematical functions linking the position of an individual within a group to

22   the risk of predation and the gains from foraging. This approach allows us to

23   investigate more closely the impact of varying parameter values on the optimal

24   position of an individual within a group. The equations were chosen to approximate

25   the shape of the curves generated by the simulation model, and were fitted by eye to

1   the general shape of the data. Variation in the parameter values results in changes

2   similar to those demonstrated by the simulation model, and the constants in each

3   equation serve to match the shape and magnitude of the resulting curve more closely

4   to the simulation results.

5

6   The costs (*C*) of occupying any given position within a group (figure 3) can be

7   described by a logistic function of the form:

8

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

10   This value represents the probability that an individual is successfully attacked by a

11   predator, given its position within the group and the number of predation events

12   relative to the size of the group.

13

14   The number of food items an individual is able to obtain, given their position within

15   the group (figure 4), can be described using a similar function:

16

17   $$F = \frac{0.1f/r}{1+e^{-100c(d-0.8)}} + \frac{f}{N}$$ (2)

18

19   The constants 0.1, 100 and 0.8 serve to approximate the shape and magnitude of

20   foraging gains curve generated by the simulation model. An individual's probability

21   of surviving is a function of the number of food items gained, and their current level

22   of satiation (*s*). A food item gained by an individual with a low satiation level

23   decreases their probability of starvation by a greater amount than the same food item

24   gained by an individual whose satiation level is already high. We calculate the

13

1 probability that an individual starves (*S*), given its current food reserves and the gains

2 from occupying any position using the following equation:

3

4
$$S = \frac{2}{1 + e^{0.5(s+F)}}$$
(3)

5

6 The fitness of an individual depends on it avoiding both predation and starvation, and

7 this is a multiplicative function (as illustrated in figure 1) of the probability that it

8 avoids starvation (1-*S*) and the probability that the individual avoids predation (1-*C*):

9

10 W = (1-*S*)(1-*C*)
(4)

11

12 The optimal position of an individual within a group is given by the value of *d* which

13 maximizes the value of *W*.

14

15 We investigate the effect of altering the parameters on the optimal position of an

16 individual in a group. In particular, we are interested in the effect of the internal state

17 variables (escape probability *a*, satiation *s*) and environmental selection pressures

18 (food availability *f*, predation risk, *P*) on optimal group position. We also investigate

19 the effects of changes in capture distance (*c*), group radius (*r*) and group size (*N*).

20

21 **Results for optimality model**

22 Our model makes a number of predictions as to how the optimal position of an

23 individual within a group varies according to the parameters of the model. We see a

24 number of intuitive results (figure 5). Firstly, as satiation level increases, or

25 probability of escaping from a predator decreases, animals preferentially occupy

14

1   central positions (figure 5a). This predicts that within a group of individuals where

2   there is variation in satiation and defense levels, there should be considerable

3   variation in optimal positions for those individuals. Central positions would be

4   occupied by satiated individuals with little chance of escaping a predator, whereas

5   peripheral positions would be occupied by hungry individuals with a good chance of

6   escaping from a predator, as predicted by the simple conceptual model of figure 1.

7

8   Figure 5a represents baseline levels: figures 5b-d represent results when a single

9   parameter value relative to figure 5a. Increasing the risk of predation (figure 5b)

10   results in an increased preference for central positions (comparing figure 5a with 5b,

11   which illustrates the effect of increasing predation risk) for any given combination of

12   satiation and escape probability. This would predict that competition for central

13   positions may increase, or groups may become increasingly compact, with reduced

14   distances between individuals. Increasing group size (but not density; figure 5c)

15   results in more uniform preferences: differences in satiation and defense levels have a

16   lower impact on position preferences in larger groups than in smaller groups, for

17   constant levels of food availability and predation risk (comparing figures 5a and 5c).

18   In this case, we would predict that animals would be competing for similar positions

19   within a group, however, preferences are for reasonably peripheral positions, and we

20   may expect the group to expand. Finally, increasing the density of the group (but not

21   the number of individuals; figure 5d) results in a shift in preference for more

22   peripheral positions (comparing figures 5a and 5d), particularly for individuals with

23   high satiation levels but low probabilities of escaping from a predator attack. High

24   densities may therefore also lead to the group spreading out, and therefore becoming

25   less dense.

1

2 The model also generates a number of less intuitive results, which suggest testable

3 predictions not yet explored in empirical systems. For example, as food availability

4 increases, preferences alter from central to peripheral positions (figure 6). Then, as

5 food availability increases further, from intermediate to high levels, the optimal

6 position shifts back to the centre again. This is likely to occur because low food

7 availability means that the foraging gains from occupying peripheral positions are not

8 sufficient to outweigh the predation costs of occupying those positions. As food

9 availability increases, the potential benefits to be gained means that individuals can

10 offset predation costs in peripheral positions. However further increases in food

11 availability mean that more food items are able to penetrate into the centre of the

12 group, and it becomes worthwhile for individuals to occupy those central positions

13 once again. As the food available to a group increases, we might expect to see the

14 group expanding and then contracting again as the optimal position preferences of

15 individuals alter.

16

17 Figures 5 and 6 show a continuum of positional preferences, from centre to edge,

18 including preferences for intermediate positions. Increasing the distance over which

19 individuals can move to capture the prey (c) can result in a different pattern appearing.

20 As capture distance increases, instead of a continuous set of preferences (figure 7a),

21 the range of satiation and defense combinations which predict intermediate optimum

22 positions decreases (figure 7b). Further increases in capture distance lead to

23 preferences for either very central or very peripheral positions (figure 7c and d).

24 When individuals can only move a short distance relative to the area of the group (low

25 c), many food items will penetrate the group, meaning that central individuals benefit

1   from avoiding predation, but are also able to gain food. If individuals can move a

2   greater distance relative to the area of the group, then individuals on the very edge of

3   the group capture all the available prey items, leaving none for the central individuals.

4   Satiated individuals (that do not need to capture food resources to ensure survival)

5   therefore benefit by positioning themselves in a location which leads to the greatest

6   avoidance of predation (the absolute centre of the group) while hungry and/or well-

7   defended individuals move to the position which affords them the greatest food

8   capture (the very edge). In this instance we might expect to see a group with a very

9   compact centre, but with reduced distances between neighbors.

10

11   **Discussion**

12   Our model illustrates a variety of potential optimum positions for individuals of

13   differing internal state, namely satiation levels and escape capabilities. We focus our

14   investigation on variations in patterns in these two internal factors, as these are the

15   most likely to vary between individuals within a group. Factors such as the

16   availability of food, the abundance of predators and the size of a group, for example,

17   are likely to be common to all group members, and represent external selection

18   pressures. If individuals within a group differ in satiation and escape capabilities, then

19   our model demonstrates that they should differ in their positional preferences. We find

20   conditions under which all individuals prefer similar locations within the group

21   (figure 5c), conditions where there is a spectrum of preferences from central to edge

22   positions (figure 5a), and conditions where there appears to be an abrupt

23   dichotomy/cut-off in preferences for central and edge positions (figure 7). To our

24   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.

1   If the majority of individuals moved to peripheral positions, for example, an isolated

2   individual in the center of a group may be at greater predation risk due to its isolation

3   and might benefit by moving towards other individuals (Hamilton, 1971), away from

4   the center of the group. A game theoretical approach where individual decisions are

5   influenced by the choices of other group members (Houston et al. 2003; Morrell 2004;

6   Morrell and Kokko 2004) would provide a more accurate picture of the dynamics of

7   spatial positioning within groups, and allow investigation of how competition for

8   positions within groups could be played out. Our model does not include this level of

9   complexity, but provides a basis upon which such a game theory model could be built,

10   and provides predictions that could be tested in empirical systems.

11

12   A final pattern that we observe from our model is one where either very central or

13   very peripheral positions are preferred (figure 7c-d). It is more difficult to predict the

14   structure of the group from this pattern, although we may expect to see groups

15   remaining together, with a cluster of individuals at the centre and others occupying

16   the periphery. In whirligig groups, for example, central individuals tend to be closely

17   packed, and nearest-neighbor distances increase towards the periphery of the group

18   (Romey 1995). Alternatively, as mentioned above, the positioning of other individuals

19   in the group may exert a strong influence on the behavior of others, causing central

20   individuals to move to more peripheral positions (to benefit from the dilution effect

21   (Foster and Treherne 1981), for example), or peripheral individuals moving into a

22   second 'tier' behind the most peripheral to reduce their predation risk (Hamilton

23   1971). Moving away from other individuals may also lead to a perceived reduction in

24   group size, altering the trade-off and changing the optimal location for an individual.

1   Empirical investigation or more complex modeling approaches could shed light on

2   how animals respond to conditions such as these.

3

4   The majority of studies looking at the effect of group positioning consider only

5   'central' versus 'peripheral' individuals, with no intermediate individuals – they are

6   either on the edge or not. Thus, there is a lack of empirical data defining the shapes of

7   the foraging and predation risk curves. However, some empirical studies suggest that

8   predators attack only the most peripheral individuals in a group. In fish attacking

9   *Daphnia* (Milinski 1977) or groups of surface-dwelling whirligigs (Romey et al.

10   2008), the predators choose only the individuals on the very edge, suggesting

11   intermediate positions are actually as safe as those in the very centre. Empirical work

12   is needed to investigate this, as our results are likely depend on the shapes of the

13   curves that are assumed to link distance from the group centre with predation risk and

14   food availability or intake. However, under certain parameter values, our model in

15   fact predicts a dichotomy between individuals that prefer central positions and those

16   that prefer edge positions. Only small alterations in their levels of satiation or escape

17   probability switch preferences from the centre to the edge, suggesting that

18   categorizing individuals as central or peripheral may be an adequate description.

19

20   Our model includes several further simplifying assumptions. Firstly, the selection

21   pressures that we considered most important to the fitness of individuals within a

22   group were predation and food distribution, but there are other factors which could

23   influence fitness and should be considered in future studies (such as energy

24   expenditure or potential for reproduction). We assume that there are foraging benefits

25   to occupying peripheral positions – our model applies to situations where groups are

1 foraging on dispersed food resources. Alternatively, groups may be centered on a food

2 resource or moving together towards aggregated resources. If this is the case, then

3 food gains are likely to be higher for centrally positioned individuals, or those leading

4 the groups. In this case, dominance will play a key role in the structuring of the group,

5 as dominants are able to monopolize access to food (Hirsch 2007), and simultaneously

6 occupy lower predation risk positions.

7

8 Our model considers only stationary groups, but in many species, moving groups are

9 common. Rather than differential predation risk and foraging gains from centre to

10 edge, these groups are likely to differ from front to back. Individuals at the front of

11 moving groups tend to have higher foraging success, and front positions tend to be

12 occupied by hungry individuals (Krause et al. 1998; Romey and Galbraith 2008).

13 There is, however, likely to be an energy cost in occupying front positions, and

14 individuals at the back can make considerable energetic savings (Krause and Ruxton

15 2002). Predation risk is also likely to vary as a function of distance from the front of a

16 group. In chub (*Semilotus atromaculatus*), individuals occupying front positions

17 suffered from greater levels of predation than individuals in rear positions (Bumann et

18 al. 1997). Front positions may therefore be equivalent to edge positions, but with the

19 added energetic costs.

20

21 Predators may also make deliberate decisions as to which individual within a group

22 prey to target, rather than attacking peripheral individuals at random (Stankowich

23 2003). Predators may more successfully track individuals at the edge of groups due to

24 the confusion effect (Neill and Cullen 1974), explaining why in some systems only

25 very peripheral individuals are attacked (Romey et al. 2008; Milinski 1977).

1   Alternatively, predators may attack individuals that are phenotypically or behaviorally

2   distinct from the rest of the group (the oddity effect; (Landeau and Terborgh 1986).

3   Sparrowhawk (*Accipiter nisus*) attacks on redshank (*Tringa totanus*) depend on

4   several behavioral factors related to the vulnerability of the prey (Quinn and

5   Cresswell 2004), rather than solely on position within the group. Isolation of

6   individuals may also be important: the selfish herd hypothesis predicts that individuals

7   are attacked in proportion to the size of their 'domain of danger', the area around each

8   individual that is closer to it than to any other individual (Hamilton 1971). The

9   perceptual ability of a predator may also limit predation risk for peripheral foragers

10 (James et al. 2004; Morrell and James 2008). Levels of anti-predator vigilance may

11 also play a role, and may differ spatially within groups (Beauchamp 2007). Higher

12 vigilance by peripheral individuals may reduce the foraging benefits associated with

13 occupying such positions, for example, leading to increased preferences for central

14 locations, or occupation of peripheral positions by more satiated individuals who have

15 less need to forage.

16

17 Individuals are likely to want to switch positions within a group. In colonial spiders

18 (*Metepeira incrassata*), larger females with egg sacs show a strong preference for

19 central positions, while younger spiders prefer peripheral positions, as they have yet

20 to attain sufficient size for successful reproduction (Rayor and Uetz 1993). If hungry

21 individuals occupy peripheral positions, then as those individuals become increasingly

22 satiated, their preference for the safer, central locations should increase, resulting in a

23 rotation of positions within a group (see also (Krause and Ruxton 2002). Such a

24 cycling of positions due to changing hunger levels can be seen in whirligig groups

25 (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

1   which may influence positioning within a group and which should be considered in

2   future approaches, including dominance hierarchies (Hirsch 2007), aggression

3   (Hemelrijk 2000), food acquisition tactics (producer-scrounger behavior; (Barta et al.

4   1997; Mónus and Barta 2008), condition-dependent predator avoidance, trade-offs

5   with other behaviors such as vigilance or mating (Houston et al. 2003; Morrell 2004;

6   Jackson and Ruxton 2006) and game theoretical approaches. Such future

7   investigations could provide a fascinating insight into the dynamics of grouping in

8   animals, extending the predictions we make here.

9

15

16   **References**

17   Baker MB, Zemel A, 2000. Josef Bertrand catches some ants: Unbiased random

18   trajectories for the simulation of position effects in groups. J Theor Biol

19   207:299-303.

20   Barta Z, Flynn R, Giraldeau LA, 1997. Geometry for a selfish foraging group: a

21   genetic algorithm approach. Proc Roy Soc Lond B 264:1233-1238.

22   Beauchamp G, 2007. Vigilance in a selfish herd. Anim Behav 73:445-451.

23   Bumann D, Krause J, Rubenstein D, 1997. Mortality risk of spatial positions in

24   animal groups: The danger of being in the front. Behaviour 134:1063-1076.

1 Clark CW, Mangel M, 2000. Dynamic state variable models in ecology: methods and
2   applications. Oxford: Oxford University Press.
3 Eisner T, 2003. For love of insects. Cambridge, Massachusetts: The Belknap Press of
4   Harvard University Press.
5 Fiske P, Rintamaki PT, Karvonen E, 1998. Mating success in lekking males: a meta-
6   analysis. Behav Ecol 9:328-338.
7 Foster WA, Treherne JE, 1981. Evidence for the dilution effect in the selfish herd
8   from fish predation on a marine insect. Nature 293:466-467.
9 Hall CL, Fedigan LM, 1997. Spatial benefits afforded by high rank in white-faced
10   capuchins. Anim Behav 53:1069-1082.
11 Hamilton WD, 1971. Geometry for the selfish herd. J Theor Biol 31:295-311.
12 Hemelrijk CK, 2000. Towards the integration of social dominance and spatial
13   structure. Anim Behav 59:1035-1048.
14 Hemelrijk CK, Kunz H, 2005. Density distribution and size sorting in fish schools: an
15   individual-based model. Behav Ecol 16:178-187.
16 Hirsch B, 2007. Costs and benefits of within-group spatial position: a feeding
17   competition model. The Quarterly Review of Biology 82:9-27.
18 Houston AI, McNamara JM, Hernandez ML, 2003. How does an individual's optimal
19   behaviour depend on its quality? An analysis based on relative ability.
20   Evolutionary Ecology Research 5:195-212.
21 Jackson AL, Ruxton GD, 2006. Toward an individual-level understanding of
22   vigilance: the role of social information. Behav Ecol 17:532-538.
23 James R, Bennett PG, Krause J, 2004. Geometry for mutualistic and selfish herds: the
24   limited domain of danger. J Theor Biol 228:107-113.

1 Krause J, 1993a. The relationship between foraging and shoal position in a mixed
2   shoal of roach (*Rutilus rutilus*) and chub (*Leuciscus cephalus*): A field study.
3   Oecologia 93:356-359.

4 Krause J, 1993b. The effect of 'Schreckstoff' on the shoaling behaviour of the
5   minnow: a test of Hamilton's selfish herd theory. Anim Behav 45:1019-1024.

6 Krause J, 1993c. Positioning behavior in fish shoals: a cost-benefit analysis. J Fish
7   Biol 43:309-314.

8 Krause J, 1994. Differential fitness returns in relation to spatial position in groups.
9   Biological Reviews of the Cambridge Philosophical Society 69:187.

10 Krause J, Hoare DJ, Croft D, Lawrence J, Ward A, Ruxton GD, Godin JGJ, James R,
11   2000. Fish shoal composition: mechanisms and constraints. Proc Roy Soc
12   Lond B 267:2011-2017.

13 Krause J, Reeves P, Hoare D, 1998. Positioning behaviour in roach shoals: The role of
14   body length and nutritional state. Behaviour 135:1031-1039.

15 Krause J, Ruxton GD, 2002. Living in Groups: Oxford University Press.

16 Krause J, Tegeder RW, 1994. The mechanism of aggregation behaviour in fish shoals:
17   individuals minimize approach time to neighbours. Anim Behav 48:353-359.

18 Krebs JR, Kacelnik A, 1991. Decision-making. In: Behavioural ecology: an
19   evolutionary approach (Krebs JR, Davies NB, eds). Oxford: Blackwell
20   Scientific Publications; 105-136.

21 Landeau L, Terborgh J, 1986. Oddity and the confusion effect in predation. Anim
22   Behav 34:1372-1380.

23 Linton MC, Crowley PH, Williams JT, Dillon PM, Aral H, Strohmeier KL, Wood C,
24   1991. Pit relocation by antlion larvae: A simple model and laboratory test.
25   Evol Ecol 5:93-104.

1   Lubin Y, Henschel JR, Baker MB, 2001. Costs of aggregation: shadow competition in

2   a sit-and-wait predator. Oikos 95:59-68.

3   Milinski M, 1977. Do all members of a swarm suffer the same predation? Zeitschrift

4   fur Tierpsychologie 45:373-388.

5   Mónus F, Barta Z, 2008. The effect of within-flock spatial position on the use of

6   social foraging tactics in free-living tree sparrows. Ethology 114:215-222.

7   Morrell LJ, 2004. Are behavioural trade-offs all they seem? Counter-intuitive

8   resolution of the conflict between two behaviours. Behav Ecol Sociobiol

9   56:539-545.

10   Morrell LJ, James R, 2008. Mechanisms for aggregation in animals: rule success

11   depends on ecological variables. Behav Ecol 19:193-201.

12   Morrell LJ, Kokko H, 2004. Can too strong female choice deteriorate male

13   ornamentation? Proc Roy Soc Lond B 271:1597-1604.

14   Morton TL, Haefner JW, Nugala V, Decino RD, Mendes L, 1994. The Selfish Herd

15   revisited: do simple movement rules reduce relative predation risk. J Theor

16   Biol 167:73-79.

17   Neill SRS, Cullen JM, 1974. Experiments on whether schooling by their prey affects

18   hunting behavior of cephalopods and fish predators. Journal Of Zoology

19   172:549-569.

20   Okamura B, 1986. Group living and the effects of spatial position in aggregations of

21   *Mytilus edulis*. Oecologia 69:341-347.

22   Parrish JK, 1989. Reexamining the selfish herd: are central fish safer. Anim Behav

23   38:1048-1053.

24   Parrish JK, Edelstein-Keshet L, 1999. Complexity, pattern, and evolutionary trade-

25   offs in animal aggregation. Science 284:99-101.

1   Parrish JK, Hamner WM, 1997. Animal groups in three dimensions. Cambridge:

2   Cambridge University Press.

3   Quinn JL, Cresswell W, 2004. Predator hunting behaviour and prey vulnerability. J

4   Anim Ecol 73:143-154.

5   Ranta E, Peuhkuri N, Laurila A, 1994. A theoretical exploration of antipredatory and

6   foraging factors promoting phenotype-assorted fish schools. Ecoscience 1:99-

7   106.

8   Rayor LS, Uetz GW, 1990. Trade-offs in foraging success and predation risk with

9   spatial position in colonial spiders. Behav Ecol Sociobiol 27:77-85.

10 Rayor LS, Uetz GW, 1993. Ontogenic shifts within the selfish herd: predation risk

11   and foraging trade-offs change with age in colonial web-building spiders.

12   Oecologia 95:1-8.

13 Romey WL, 1995. Position preferences within groups: Do whirligigs select positions

14   which balance feeding opportunities with predator avoidance. Behav Ecol

15   Sociobiol 37:195-200.

16 Romey WL, 1996. Individual differences make a difference in the trajectories of

17   simulated schools of fish. Ecological Modelling 92:65-77.

18 Romey WL, 1997. Inside or outside: testing evolutionary predictions of positional

19   effects. In: Animal groups in three dimensions (Parrish JK, Hamner WM, eds):

20   Cambridge University Press; 174-193.

21 Romey WL, Galbraith E, 2008. Optimal group positioning after a predator attack: the

22   influence of speed, sex, and satiation within mobile whirligig swarms. Behav

23   Ecol In Press.

24 Romey WL, Wallace AC, 2007. Sex and the selfish herd: sexual segregation within

25   nonmating whirligig groups. Behav Ecol (in press).

1   Romey WL, Walston A, Watt PJ, 2008. Do 3-D predators attack the margins of 2-D

2   selfish herds? Behav Ecol 19:74-78.

3   Ruckstuhl KE, Neuhaus P, 2005. Sexual Segregation in Vertebrates: Ecology of the

4   Two Sexes. Cambridge: Cambridge University Press.

5   Šálek M, Šmilauer P, 2002. Predation on Northern Lapwing *Vanellus vanellus* nests:

6   The effect of population density and spatial distribution of nests. Ardea 90:51-

7   60.

8   Stankowich T, 2003. Marginal predation methodologies and the importance of

9   predator preferences. Anim Behav 66:589-599.

10   Tosh CR, Jackson AL, Ruxton GD, 2006. The confusion effect in predatory neural

11   networks. Am Nat 167:E52-E65.

12   Vine I, 1971. Risk of visual detection and pursuit by a predator and selective

13   advantage of flocking behaviour. J Theor Biol 30:405-422.

14   Viscido SV, Miller M, Wethey DS, 2002. The dilemma of the selfish herd: The search

15   for a realistic movement rule. J Theor Biol 217:183-194.

16   Viscido SV, Wethey DS, 2002. Quantitative analysis of fiddler crab flock movement:

17   evidence for 'selfish herd' behaviour. Anim Behav 63:735-741.

18   Watt PJ, Nottingham SF, Young S, 1997. Toad tadpole aggregation behaviour:

19   evidence for a predator avoidance function. Anim Behav 54:865-872.

20   Wilson DS, 1974. Prey capture and competition in the ant lion. Biotropica 6:187-193.

21

1   **Figure legends**

2   **Figure 1: a)** Conceptual model relating fitness to the distance from the centre of the

3   group. Food availability and risk of predation increase with distance from centre, for

4   individuals that are hungry or satiated and at low (defended) or high (vulnerable risk

5   of predation. **b)** Graph of combined fitness due to multiplicative effects of a given

6   combination of food availability and predation risk (e.g.: defended x hungry). Filled

7   circles and dropped lines indicate the optimum distance from the centre for each type

8   of individual.

9

10   Figure 2: N individuals (black filled circles, here N=10) are placed within a circle of

11   radius r (solid edged circle). Each individual is a distance d from the centre of the

12   circle. **a)** Predators, P (large checkerboard circle, here P=2) appear at random within a

13   circle of radius R (dashed circle) and attack the nearest individual (solid arrow). **b)**

14   Each individual can move a distance c to capture food items (dotted circles

15   surrounding the individuals). Food items (f) enter from the outside of the group

16   (dashed lines) and are intercepted by individuals at the solid diamond. Note that

17   figures 2a and 2b are drawn to different scales.

18

19   **Figure 3**: Effect of varying parameters on the link between occupied position (x-axis)

20   and per capita risk of predation (y axis) in the simulation model. **a)** Varying group

21   size (N). Filled squares: N=10, filled circles: N=20, open squares: N=50, open circles,

22   N=100. **b)** Varying number of predators (P). Filled squares: P=1, filled circles: P=2,

23   open squares: P=5, open circles, P=10. **c)** Varying the probability an individual

24   evades a predator attack (a). Filled squares: a=0, filled circles: a=0.2, open squares:

25   a=0.4, open circles, a=0.6. **d)** Varying the radius of the circle formed by the group (r:

1 equivalent to varying density). Filled squares: r=1.128, filled circles: r=1.596, open

2 squares: r=2.253, open circles, r=3.568. For each panel, all other parameter values

3 are: N=20, P=2, a=0.2, r=1.595. Distances from the centre are scaled between 0 and 1

4 (zero being the centre and 1 being the maximum value of r) to allow comparisons to

5 be made between figure panels.

6

7 **Figure 4:** Effect of varying parameters on the number of food items captured in the

8 simulation. **a)** Varying group size (N). Filled squares: N=10, filled circles: N=20, open

9 squares: N=50, open circles, N=100. **b)** Varying number of food items (f). Filled

10 squares: f=10, filled circles: f=20, open squares: f=50, open circles, N=100. **c)** Varying

11 the distance over which an individual can capture a food item (c). Filled squares:

12 c=0.05, filled circles: c=0.1, open squares: c=0.2, open circles, c=0.3. **d)** Varying the

13 radius of the circle formed by the group (r: equivalent to varying density). Filled

14 squares: r=1, filled circles: r=2, open squares: r=5, open circles, r=10. For each panel,

15 all other parameter values are: N=20, f=20, c=0.2, r=1.595. Distances from the centre

16 are scaled between 0 and 1 (zero being the centre and 1 being the maximum value of

17 r) to allow comparisons to be made between figure panels.

18

19 **Figure 5:** Results of the model. **a)** The effect of increasing levels of satiation (s; x-

20 axis) and probability of escaping a predator (a; y-axis). Shading indicates the optimal

21 distance from the group centre of an individual with each combination of satiation (s)

22 and escape probability (a), where black indicates central positions (d = 0) and white

23 indicates peripheral positions (d = 1; all panels). Parameter values used: N=10, P=2,

24 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)** $c=0.15$.
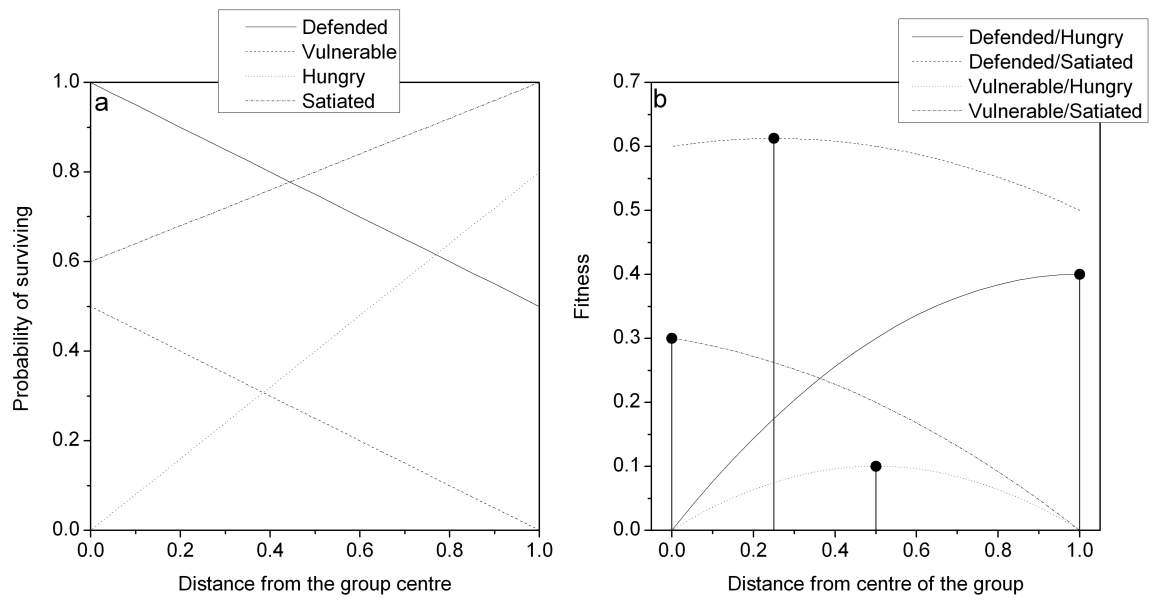
1 **Table 1:** Parameters used in the models. Information in parentheses relates to the
2 simulation model only.
3

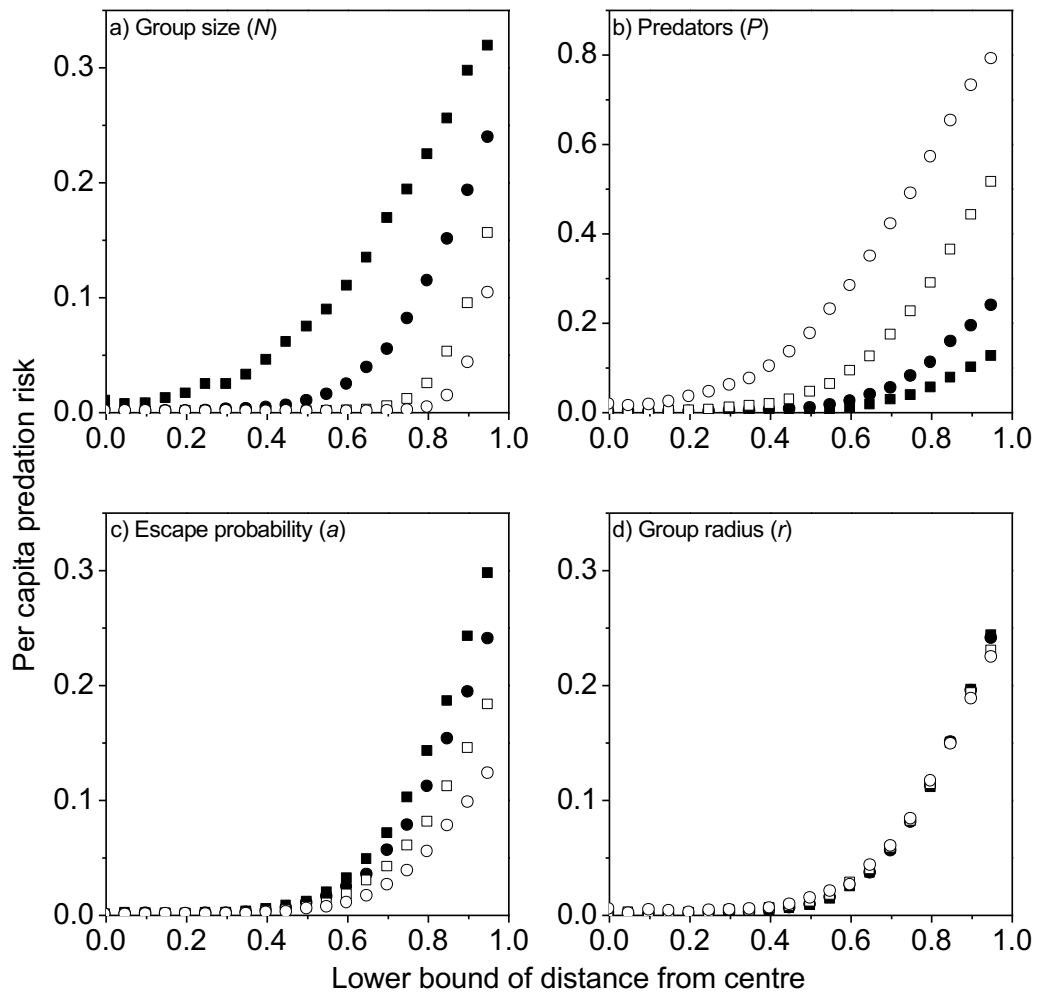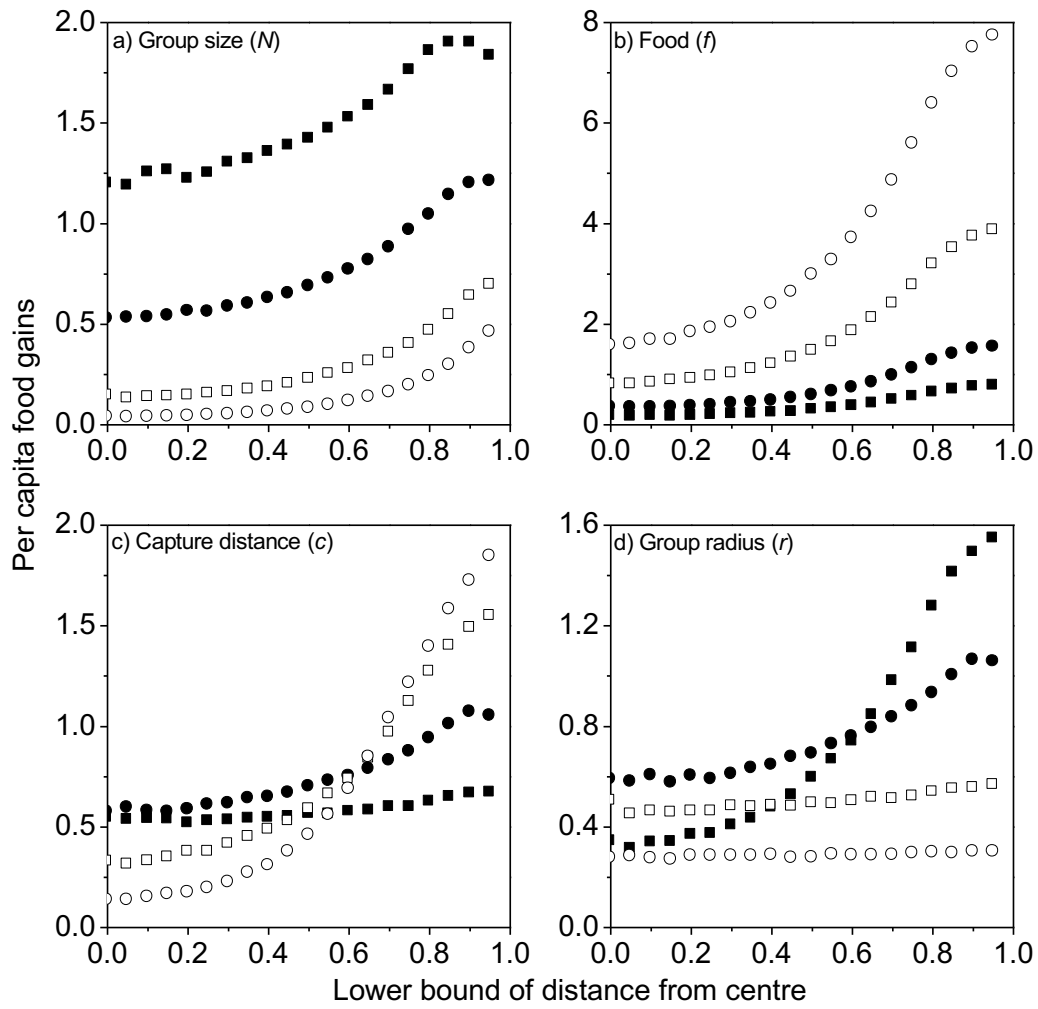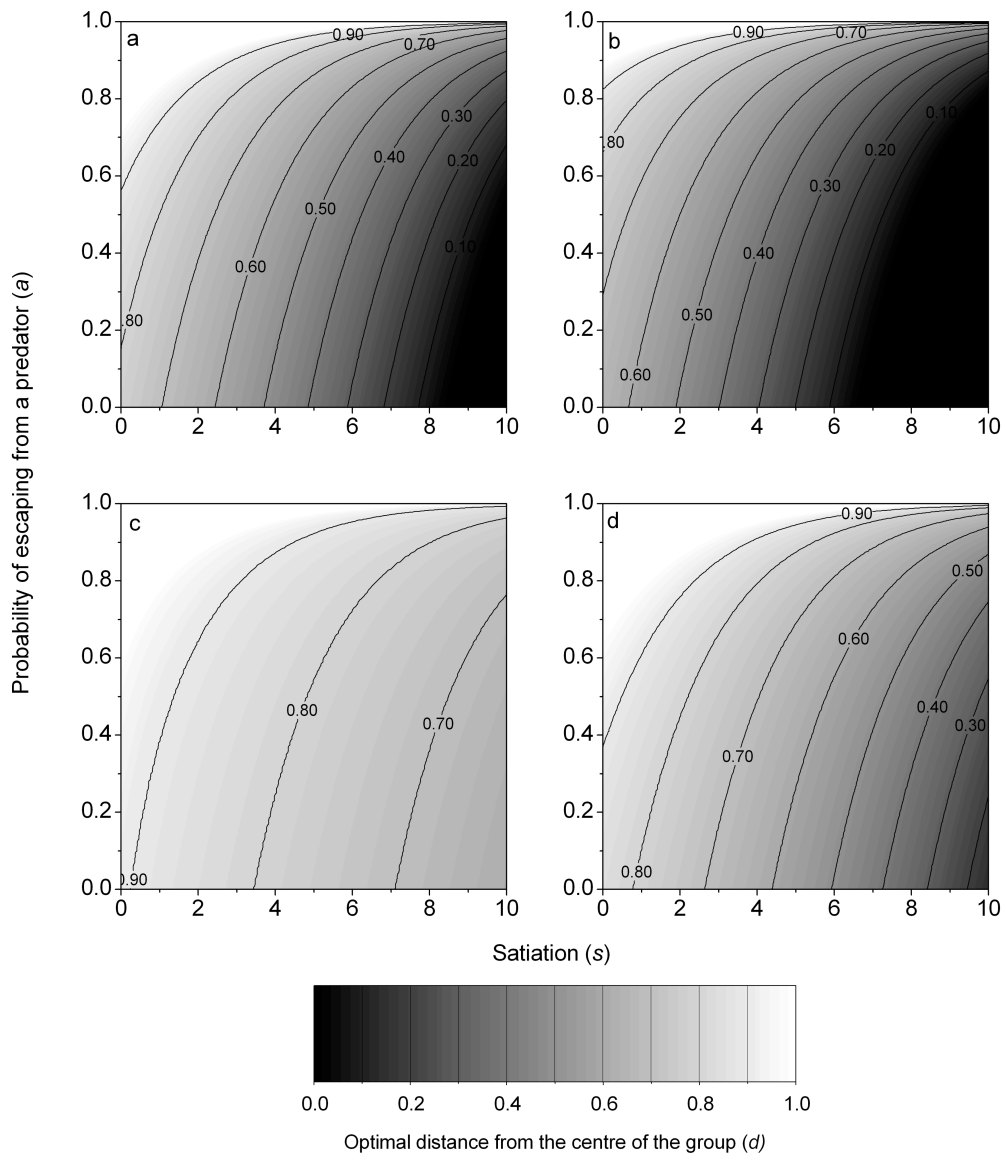| Parameter	Description
N	Number of individuals
d	Distance from the centre of the group
r	Radius of the circle in which the prey are positioned
P	Predation risk (number of predation events)
R	(Radius in which predators are positioned)
a	Probability that an individual avoids a predation attempt
f	Number of food items available
α_f	Angle used for calculating food trajectory
d_f	Distance used for calculating food trajectory
c	Distance individuals can move to capture the prey
C	Costs of occupying any given position within a group
F	Foraging gains from occupying any position within a group
B	Benefits of occupying any position within a group
W	Fitness of an individual

4
5

Figure 1

Figure 2

Figure 3

2

a) Group size (*N*)

b) Food (*f*)

c) Capture distance (*c*)

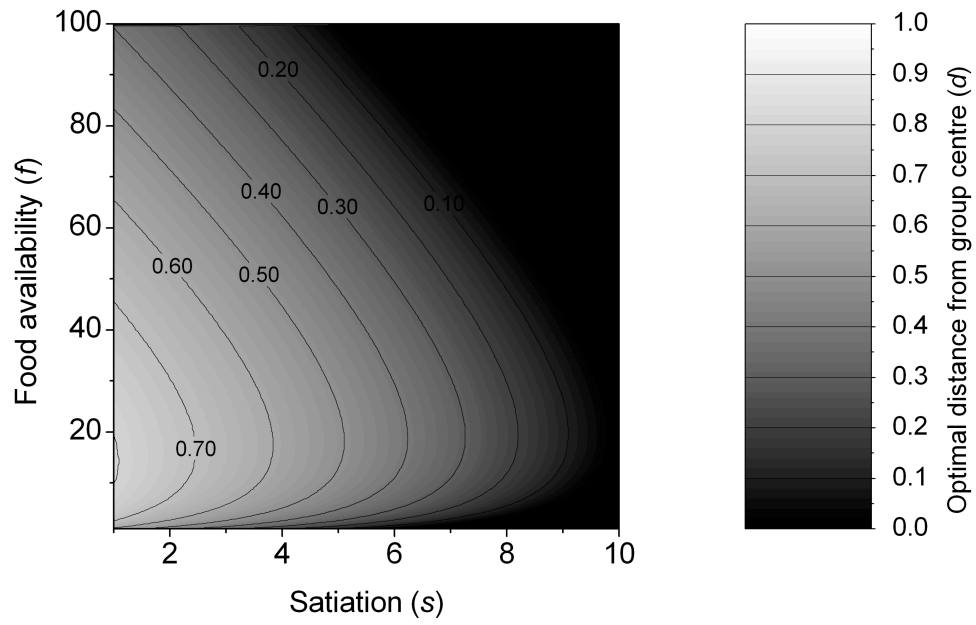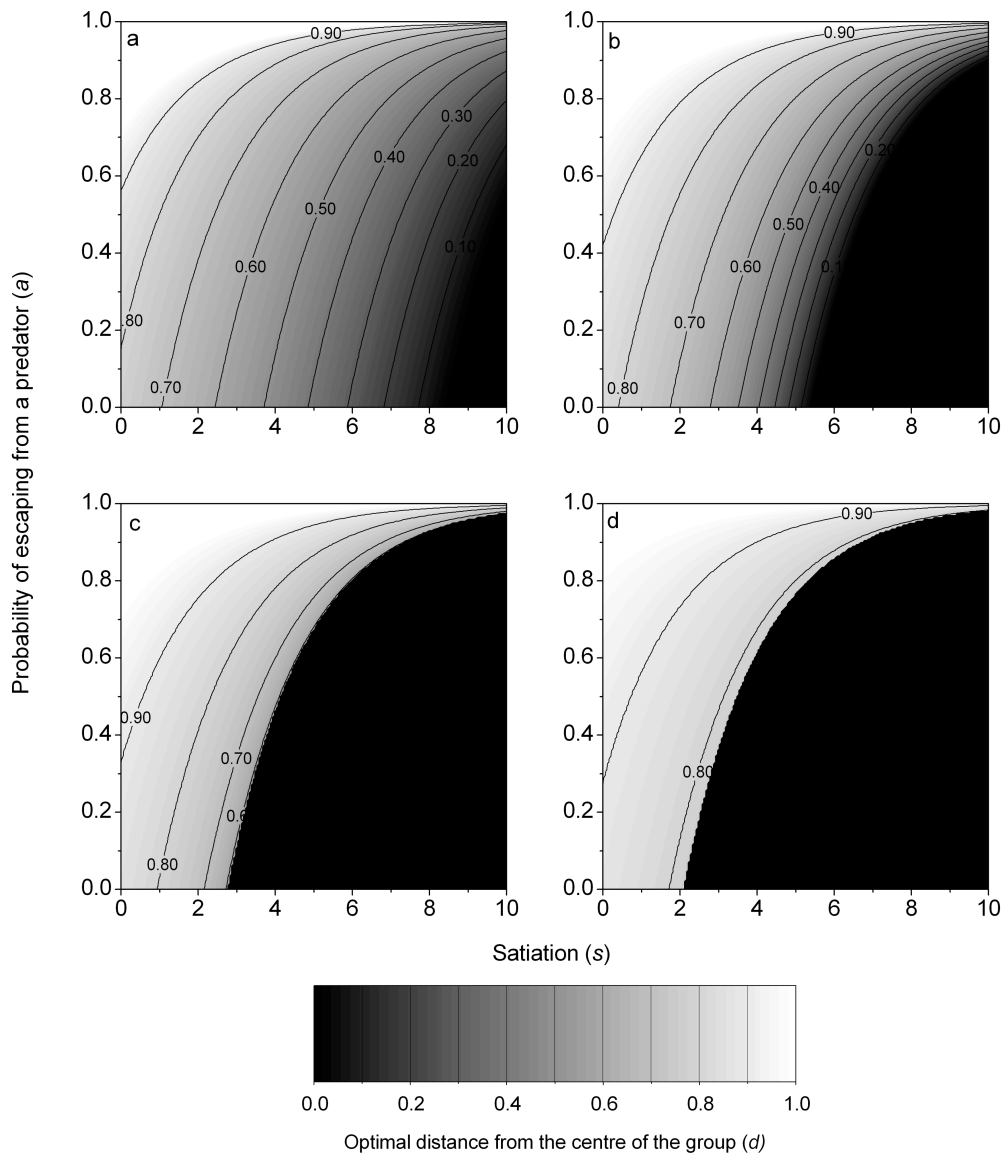d) Group radius (*r*)

Per capita food gains

Lower bound of distance from centre

3
4

Figure 4

1   **Figure 5**

2

Figure 6

Optimal distance from the centre of the group (*d*)