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## Antipredator vigilance in birds: Modelling the ‘edge’ effect

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### Abstract

Many animals spend a large proportion of their time either foraging for food or watching out for predators (antipredator vigilance). There have been many theoretical and empirical studies investigating the trade-off between these two activities, especially in birds. Previous models of antipredator vigilance assume that all birds within the group spend the same amount of time feeding. However, many empirical studies have shown that individuals on the edge of flocks are more vigilant. Here we describe a vigilance model which investigates the effect of position on the birds’ strategies by dividing the feeding area into an inner and outer region. The model examines how various parameters such as food availability and predation risk affect the strategies of individual birds according to whether they are in the inner or outer region. Our model predicts that birds in the outer group are always more vigilant than those in the inner region. Birds in the centre receive a higher payoff in each of the wide range of scenarios that we have considered, and so our model also indicates why dominant birds would choose to feed in the centre of the group; a prediction in accord with several empirical studies.

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*Keywords:* Vigilance; Edge effect; Communication; Evolutionarily stable strategies; Group living

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## 1. Introduction

Many animals spend a large proportion of their time either foraging for food or watching out for predators. Often these two tasks are mutually exclusive, especially for ground-feeding birds which must look down to search for food, but look upwards to see approaching predators, such as hawks. The trade-off between these two activities has been extensively studied, especially in birds (e.g. [1–3]). Many species feed in groups so that individuals can benefit from the vigilance of other members of the group [4,5] and also benefit from the ‘dilution effect’ whereby the larger the group, the less likely a particular animal is to be killed [6,7]. However, it is also possible that larger groups may attract more predators, offsetting the advantages of the ‘dilution effect’.

Many mathematical models of antipredator vigilance in birds have been developed (e.g. [2,3,8–11]). Most models seek to predict the optimal time that birds should spend feeding versus the time spent being vigilant. Proctor and Broom [12] also considered the area of the flock as a strategic variable under natural selection. This model assumed that it took longer for individuals feeding in large areas to scan for predators as they had a wider region to survey. Proctor et al. [8] modified this model and assumed that the cost of a large area was that if individuals were spread over a large area, then communication between flock members would be poor. This idea was based on studies which showed that near individuals make better vigilance mates [13,14].

In our previous model [8], we assumed that all birds within the group scanned at the same rate, regardless of their position. Lazarus [15] suggests that individuals on the flock periphery are at a greater risk of capture since they will be encountered first by an approaching ground predator and if attacked from the air, they may be selected because of their relative isolation. As a result, we would expect individuals on the edge of the flock to be more vigilant. Studies have in fact shown that birds on the edge of the group spend more time being vigilant than those in the centre (e.g. [16]). This is often referred to as the ‘edge’ effect [17]. Therefore, we developed a model which explores the effect of position within the flock on evolutionarily stable vigilance rates. We assumed that a flock of foraging birds are feeding in an area which has an inner or centre region and an outer or edge region. So we have two groups of birds within the flock and we sought to find the best vigilance rate and the best area for each group.

Lazarus [15] also suggests that if birds in some peripheral zone of the flock were more vigilant, then the proportion of birds vigilant would decline as flock size increased since the number of birds in this zone would represent a diminishing proportion of the whole flock. Lazarus [15] developed a rigorous argument to show that this is the case, based on the assumption that bird density is constant throughout the flock and for all flock sizes. We do not make such an assumption, but rather allow the birds in our model flocks to arrange themselves so as to gain best individual advantage. The density of birds in different parts of the flock then becomes a (testable) model prediction rather than an assumption.

As well as predation risk, it has been observed that food availability may also depend on group position. For example, Barnard and Thompson [18] found that worm density increased near the flock periphery. This suggests that there may be a trade-off between feeding in the safer centre of the group where food is less abundant, or feeding at the edge where food is in better supply but predation risk is high. Whitfield [19] observed that dominance relationships in wading birds can result in the juveniles often ending up on the edges of flocks and being more often caught by predators. This phenomenon has also been observed among willow tits, *Parus montanus*, where

dominants usually occupied sites near the centres of trees, while subordinates were forced to the outer parts, where they spent more time on vigilance but were still more often captured by pygmy owls, *Glaucidium passerinum* [20].

A major problem in interpreting studies of the effect of position in the group on vigilance behaviour is that different definitions are used for edge and centre groups. In some studies (e.g. [21]), small groups and edge birds were put into one category. Krause [22] suggested that if an aerial view could be obtained, individuals can be defined as peripheral if they are at a vertex of the smallest closed convex polygon enclosing all members of the group. Another definition put forward by Barnard and Thompson [18] is that ‘edge’ birds are those with no companions between themselves and the border of the field. Although these definitions enable an observer to categorise each bird into each group fairly easily, they were not suitable for our model. Instead we assumed that the feeding region is circular and we split the region into an inner circular region and an outer ring shaped region. We looked for evolutionarily stable strategies (ESSs) [23], restricting ourselves to considering solutions where all birds within a region scan at the same rate, but that the inner birds can scan at a different rate to the outer birds. Obviously, there are infinite number of ways in which we can split the area between the two groups and so it was necessary to make some simplifying assumptions.

We investigate whether our model always predicts that outer birds are more vigilant than inner birds and whether flock density should be the same for the inner and outer birds. We also consider how differences in food availability and predation risk affect the predictions. In addition, we see how changing different parameters common to both groups, such as the predation rate and the total group size, affects the behaviour in our model.

## 2. The model

Since our model is based on Proctor et al. [8], it is necessary to briefly describe this model. Proctor et al. [8] considered a flock of  $N$  birds feeding in a region of area  $A$ . Just as birds have to find the right balance between feeding and scanning, so there is a trade-off between utilising large and small areas. The assumptions of the model are

- The predator attacks at rate  $y$  and targets a particular individual, with each individual having the same probability of being chosen.
- The predator requires a certain time for it to attack,  $t_a$ , which is the time from when it can be detected by the prey to when it reaches a distance when the prey can no longer escape.
- The predator will be spotted by any individual that scans during this interval, scans being of length  $t_s$ .
- The probability that any individual spots the predator is given by

$$P = 1 - u \exp \left[ -b \left( \frac{1}{u} - 1 \right) \right],$$

where  $u$  is the proportion of time spent feeding and  $b = t_a/t_s$  [11].

- If any individual spots the predator, it will pass on the information to another particular individual with a probability  $P_A$ , with this probability decreasing as the area increases. We define  $P_A = \frac{1}{1+(\gamma A)^d}$ , where  $\gamma$  and  $d$  are positive real numbers.
- The probability that any individual is informed of an attack by each member of the flock is  $PP_A$ .
- The cost of an attack,  $K$ , is equivalent to the amount of energy lost if a bird is attacked and killed. This was assumed to be the amount of energy it would have acquired if it had survived through a season. Thus, death is equivalent to having energy level zero. (See [8] for a fuller explanation of why we modelled the cost of vigilance as an energetic cost.)
- The rate of food uptake depends on the area,  $A$ , the flock size,  $N$ , and the area that a bird requires to feed at half its capacity,  $Z$  and is given by  $\left(1 - \frac{1}{1+(A/NZ)^m}\right)\theta$ , where  $m$  is a measure of how fast the feeding rate increases with area and  $\theta$  is the maximum feeding rate.

In this paper, we modify Proctor et al.'s [8] model, and divide the feeding area into an inner and outer region of area  $A_1$  and  $A_2$ , respectively. We first pick the area by choosing the smallest circle that encloses the whole group. We assume that at least two birds are close to the edge. We then divide the region into an outer and an inner region. We denote the number of birds in each region by  $N_1$  and  $N_2$ . There is necessarily a constraint that  $N_2$  is at least one, otherwise if the outer region is empty, the total area of the group is equal to the area of the inner region. Since it is possible that food density is different in each region, we assume that each region has a different value of  $Z$ , the area required for a bird to feed at half its maximum capacity, which we denote by  $Z_1$  and  $Z_2$ . We assume that the model parameters,  $m$ ,  $\gamma$ ,  $K$ ,  $\theta$  are independent of group position. We assume initially that  $b = t_a/t_s$  is independent of group position but later consider the possibility that the time taken for a scan is affected by position. Lastly, we consider the probability of passing on the information,  $P_A$ . There are four situations in which information can be passed on. Firstly, an inner bird can inform another inner bird; secondly an inner bird can inform an outer bird; thirdly an outer bird can inform an inner bird; and lastly an outer bird can inform another outer bird. The second and third cases can reasonably be considered as the same, so we need only consider three cases. We assume that the probability of passing on information is independent of the number of birds in each region. In this case, since the inner birds taken by themselves occupy a smaller area than the whole group, the probability of passing on the information from an inner to an inner should be greater than in the other two cases. Denoting this by  $P_A^{(1)}$ , an obvious formula is

$$P_A^{(1)} = \frac{1}{1 + (\gamma A_1)^d}.$$

For the information transfer between an inner and outer bird, we define  $P_A^{(2)}$  as

$$P_A^{(2)} = \frac{1}{1 + (\gamma(A_1 + A_2))^d}.$$

When an outer bird informs another outer bird, then it is possible that the two birds are close together, but on the other hand, they might be on opposite sides of the group. So the probability of information transfer between two outer birds depends on the total area and not just the area of

the outer group. The mean distance between two outer birds is approximately the same as the mean distance between an inner and an outer bird (although the variance will be larger) and so for modelling simplicity, we assume that  $P_A^{(3)} = P_A^{(2)}$ , where  $P_A^{(3)}$  is the probability of an outer bird informing another outer. We assume that the parameters  $\gamma$  and  $d$  are the same in all cases. It should be noted that when group sizes are large, there will be a large variability in the distance between two outer birds, so that a more complicated model may be required in which we only consider that information can be transferred between near neighbours.

The likelihood of a bird being the individual targeted by the predator will depend on whether it is in the inner or outer group. We let

$$P \text{ [inner targeted]} = 1/(N_1 + \tau N_2)$$

and

$$P \text{ [outer targeted]} = \tau/(N_1 + \tau N_2),$$

where  $\tau$  is a positive real number, and in general  $\tau \geq 1$ . For example, if  $\tau = 2$ , then a given outer bird is twice as likely to be targeted as a given inner bird.

As in [8], we chose  $m = 5$ ,  $\gamma = 0.04$ ,  $d = 3$ ,  $t_a = 2$  s,  $t_s = 1$  s,  $y = 0.00005$  s<sup>-1</sup>,  $K = 10^7$  J, and  $\theta = 10$  J s<sup>-1</sup> as our ‘default’ parameters. The ‘default’ parameters were based on empirical data and are discussed in detail in [8,12]. We start by considering a flock of size  $N = 20$ . Initially we let  $Z_1 = 1.0$  and  $Z_2 = 1.0$ , so that the quality of the food source is the same for both inner and outer birds. We later vary the ratio  $Z_1:Z_2$  to allow either the inner birds or the outer birds to have a better food source. We assume that birds occupy a circular region and imagine that we draw a circle to enclose the flock. We then draw a smaller concentric circle with a radius half that of the larger circle. The smaller circle corresponds to the inner region, and the remaining ring-shaped region corresponds to the outer region. By simple geometry, the outer region is three times larger than the inner region and so if the total area is 20 m<sup>2</sup> for example, then  $A_1 = 5$ ,  $A_2 = 15$ . This method of dividing the region is reasonable for small flock sizes but we change this assumption for large areas when considering larger flock sizes (see Section 2.2.4). We initially let  $\tau = 1$  for the default value so that each bird has an equal probability of being targeted regardless of its position. In Section 2.1, we use the same fitness function as in our previous models [8,12], this being based on the earlier model described by Broom and Ruxton [9]. The function  $H = F - G$ , seeks to find the optimum trade-off between foraging and avoiding predation, where  $F$  is the rate of energy gained per second due to feeding and  $G$  is the energy lost per second due to predation.

## 2.1. Evolutionarily stable strategies

We consider a group where all individuals play  $(u_1^*, u_2^*)$  allowing a single mutant, in either the inner or outer group, to vary its vigilance level. There are two cases.

### 2.1.1. Case 1: the mutant is an inner bird

We assume that an inner mutant feeds for a proportion of time  $v$ , while the rest of the inner group feeds for a proportion of time  $u_1$ , and the outer group feed for a proportion  $u_2$ . The fitness

of each individual depends on whether it is a non-mutant inner bird, an outer bird or the mutant bird. To find the ESS, we need only consider the fitness of the mutant bird, and whether it does better than if it played the majority strategy. We denote this fitness by  $H_1$ , where

$$H_1(u_1, u_2, v) = F_1(v) - G_1(u_1, u_2, v)$$

with

$$F_1(v) = \theta v \left( 1 - \frac{1}{1 + (A_1/N_1 Z_1)^m} \right);$$

$$G_1(u_1, u_2, v) = yK(1 - P_3)(1 - P_1 P_A^{(1)})^{N_1-1} (1 - P_2 P_A^{(2)})^{N_2} \frac{1}{N_1 + \tau N_2};$$

and

$$P_1 = 1 - u_1 \exp \left[ -b \left( \frac{1}{u_1} - 1 \right) \right], \quad P_2 = 1 - u_2 \exp \left[ -b \left( \frac{1}{u_2} - 1 \right) \right],$$

$$P_3 = 1 - v \exp \left[ -b \left( \frac{1}{v} - 1 \right) \right],$$

where  $P_1$ ,  $P_2$ , and  $P_3$  are the probabilities that the inner non-mutant, outer, or mutant spots the predator respectively. At the ESS, if the inner group is feeding for a proportion of time  $u_1^*$ , then the mutant's best response is also to feed for a proportion of time  $u_1^*$ , and similarly for a mutant in the outer group. If we assume that the population plays  $(u_1^*, u_2^*)$ , then we need

$$H_1(u_1^*, u_2^*, u_1^*) \geq H_1(u_1^*, u_2^*, v) \quad \forall v.$$

### 2.1.2. Case 2: the mutant is an outer bird

If a single mutant in the outer group feeds for a proportion of time  $v$ , then the fitness of this individual is given by

$$H_2(u_1, u_2, v) = F_2(v) - G_2(u_1, u_2, v),$$

where

$$F_2(v) = \theta v \left( 1 - \frac{1}{1 + (A_2/N_2 Z_2)^m} \right);$$

and

$$G_2(u_1, u_2, v) = yK(1 - P_3)(1 - P_2 P_A^{(3)})^{N_2-1} (1 - P_1 P_A^{(2)})^{N_1} \frac{\tau}{N_1 + \tau N_2}.$$

As in case 1, we need

$$H_2(u_1^*, u_2^*, u_2^*) \geq H_2(u_1^*, u_2^*, v) \quad \forall v.$$

### 2.1.3. Finding the ESS

Since the mutant can be in either the inner or outer group, we need to solve both

$$H_1(u_1^*, u_2^*, u_1^*) \geq H_1(u_1^*, u_2^*, v) \quad \text{and} \quad H_2(u_1^*, u_2^*, u_2^*) \geq H_2(u_1^*, u_2^*, v),$$

which implies that

$$\begin{aligned} \frac{\partial}{\partial v} H_1(u_1^*, u_2^*, v) &= 0 \quad \text{at } v = u_1^*; \\ \frac{\partial}{\partial v} H_2(u_1^*, u_2^*, v) &= 0 \quad \text{at } v = u_2^*. \end{aligned}$$

Calculating both these partial derivatives gives:

$$\begin{aligned} \frac{\partial}{\partial v} H_1(u_1^*, u_2^*, v) &= \theta \left( 1 - \frac{1}{1 + (A_1/N_1 Z_1)^m} \right) + yKP'_3(1 - P_1 P_A^{(1)})^{N_1-1} (1 - P_2 P_A^{(2)})^{N_2} \frac{1}{N_1 + \tau N_2}; \\ \frac{\partial}{\partial v} H_2(u_1^*, u_2^*, v) &= \theta \left( 1 - \frac{1}{1 + (A_2/N_2 Z_2)^m} \right) + yKP'_3(1 - P_2 P_A^{(3)})^{N_2-1} (1 - P_1 P_A^{(2)})^{N_1} \frac{\tau}{N_1 + \tau N_2}, \end{aligned}$$

where

$$P'_3 = -\exp \left[ -b \left( \frac{1}{v} - 1 \right) \right] \left( 1 + \frac{b}{v} \right).$$

If the mutant is an inner bird, then for each  $u_2^*$ , we can find the value of  $u_1^*$  for which  $\frac{\partial}{\partial v} H_1 = 0$ . Similarly if the mutant is an outer bird, then for each  $u_1^*$ , we can find the value of  $u_2^*$  for which  $\frac{\partial}{\partial v} H_2 = 0$ . We solved these equations using routines in SPlus for a given pair  $(N_1, N_2)$ . To obtain the stable values of  $N_1$  and  $N_2$ , we found the values where it would not pay any bird to move region (see Appendix A for further details). We obtain the area sizes by finding the area which maximises the total reward value using the above scheme. For the sake of computability we reduce our consideration to integer-valued areas only. With the default parameters, we obtained the best area to be  $A_1 = 9 \text{ m}^2$  and  $A_2 = 27 \text{ m}^2$ , with an arrangement of six birds in the inner region and 14 birds in the outer region. The inner birds spend about 98% of their time feeding and 2% of their time being vigilant; the outer birds spend about 82% of their time feeding and 18% of their time being vigilant. The outer birds also have more space to feed (approximately  $2 \text{ m}^2$  per bird compared to  $1.5 \text{ m}^2$  for inner birds). So, the model predicts that the outer birds are more vigilant which agrees with experimental data [16,24] even in the absence of a difference in predation risk. The rest of the details can be seen in Table 1 below. Our previous model [8] predicted that for a flock of 20 birds, the best total area is  $36 \text{ m}^2$  and that birds spend 86% of their time feeding and 14% of their time being vigilant with a payoff of 5.74 per bird. The main difference in the models is that if inner and

Table 1  
The best arrangement of groups for different areas

$A_1$	$A_2$	$N_1$	$N_2$	$u_1$	$u_2$	Inner individual payoff	Outer individual payoff	Total group payoff
5	15	5	15	1.000	0.910	3.41	3.13	63.99
6	18	5	15	1.000	0.902	4.79	4.43	90.42
7	21	5	15	0.995	0.885	5.60	5.18	105.64
8	24	5	15	0.989	0.860	6.04	5.48	112.55
9	27	6	14	0.977	0.819	5.80	5.60	113.22
10	30	7	13	0.969	0.764	5.59	5.44	109.89
11	33	8	12	0.962	0.699	5.40	5.15	104.92



outer birds are allowed to use different vigilance strategies, then inner birds can spend more time feeding and increase their payoff and so benefit from the increased vigilance of the outer birds.

## 2.2. Varying the model parameters

We only vary the parameters that obviously depend on group position since the effect of varying other parameters has been explored elsewhere [8]. These are the relative food availability ( $Z_1/Z_2$ ) and the relative predation risk ( $\tau$ ). Although the predator attack rate does not depend on group position, we know from our previous models that an increase in attack rate leads to an increase in vigilance levels and a lowering of the payoffs. We vary the attack rate to see if these effects occur for both the inner and outer groups. We consider both the case when the predation risk is the same for both groups, and also when it is safer in the centre. We also look at the possibility that the centre group is safer but has less food available since Petit and Bildstein [25] found this to be the case in a study of the foraging behaviour of white ibises, *Eudocimus albus*.

### 2.2.1. Food quantity and quality depends on position

The parameters  $Z_1$  and  $Z_2$  in our models are a measure of the area required per bird in order to feed at half the maximum rate, for the inner and outer regions, respectively. These parameters depend on both the density of food and the quality of food within each region. We might expect that the food source is more abundant in the centre of the feeding area since the first birds to arrive in the area would start to feed on the best patch, and later arrivals are more likely to arrive at the edge of the flock. However, some studies suggest that there is a better food source around the edge. For instance, a study of white ibises, *Eudocimus albus*, foraging for crabs on mudflats showed that edge birds were able to visually detect and chase crabs on the surface, whereas centre birds had to repeatedly probe holes for hidden crabs [25]. Keys and Dugatkin [21] studied the effect of position on the foraging behaviour of starlings and found that the edge birds attained the same rate of prey intake as centre birds which were less vigilant, suggesting that prey abundance may have been lower in the centre of flocks. They suggested that this may be due to a greater overlap of search paths in the centre than at the edge, since the flocks they studied tended to remain stationary. The quality of food may also depend on position. For example, Black et al. [26] found that edge individuals in geese flocks fed on higher quality food, (clover rather than grass), than centre birds.

Therefore, we vary the ratio  $Z_1:Z_2$  to see how the model predictions are affected when either the centre or the edge group has a better food source. In the first case, we allow  $Z_1/Z_2 = 0.5$ , so that the inner region has a food source which is twice as profitable as the outer region; and in the second case  $Z_1/Z_2 = 2$ , so that the outer region is twice as good as the inner. In each case we fix  $Z_2 = 1$  and vary the value of  $Z_1$ . The results are shown below in Fig. 1(a) from which we can compare the model predictions to the case when  $Z_1 = Z_2$ .

When the inner region has a better food source, then the model predicts that a smaller area is required and that more birds feed in the inner region, so that the density of the inner birds has increased. The density of the outer birds is almost unchanged. The inner birds are being slightly less vigilant and receive a higher payoff. The outer birds also spend more time feeding and receive a higher payoff. This could be due either to the smaller feeding areas and hence increase in safety, or the need to compensate for the poorer food source. The decrease in vigilance has been



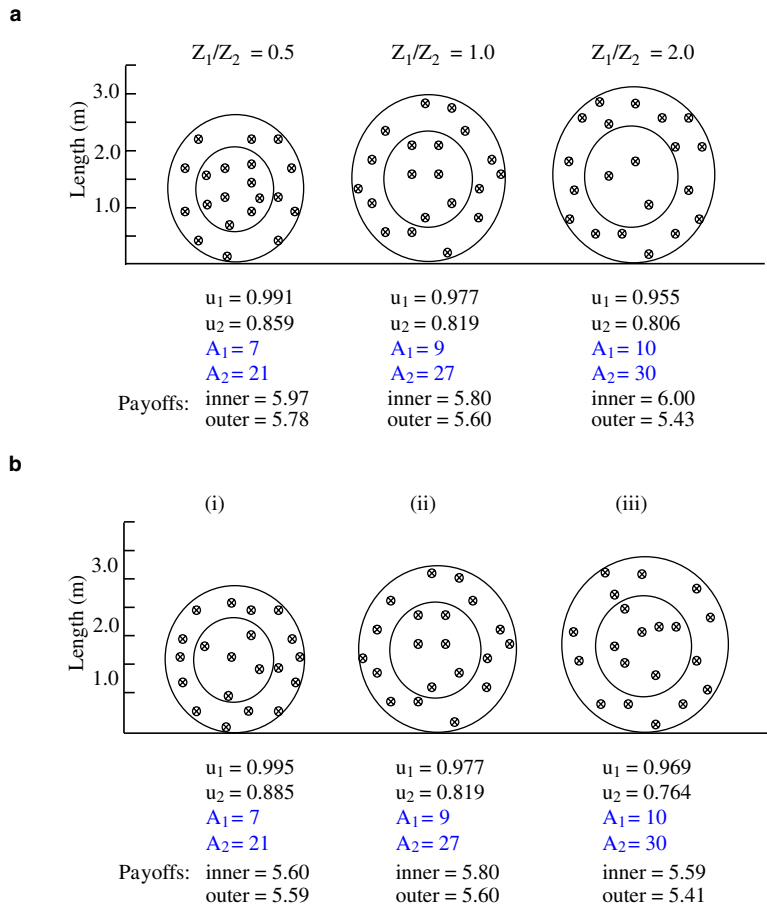


Fig. 1. (a) How the strategy for the proportion of time spent feeding ( $u_1, u_2$ ), area ( $A_1, A_2$ ) and arrangement of birds ( $N_1, N_2$ ) changes with the ratio  $Z_1/Z_2$ . (b) The best strategy ( $u_1, u_2$ ), and arrangement of birds ( $N_1, N_2$ ) when  $Z_1/Z_2 = 1$  for the optimal areas obtained in (a) when (i)  $Z_1/Z_2 = 0.5$ ; (ii)  $Z_1/Z_2 = 1.0$ ; (iii)  $Z_1/Z_2 = 2.0$ .

compensated for by the smaller area which has increased the probability of being informed of an attack, so the costs of an attack have gone down.

When the outer region has a better food source, then the model predicts that a larger area is required and that only three birds should be in the inner region with 17 in the outer. As a result the inner birds are more spread out and the outer birds are closer together. Both the inner birds and the outer birds spend less time feeding, when the outer region has a better food source. Despite the fact that they are feeding less, the inner birds are doing better. As expected the outer birds do worse, and the flock as a whole has a smaller payoff.

Since altering the ratio  $Z_1/Z_2$  affects the optimal area for the groups, then it is possible that the model predictions are due to the change in the efficiency of information transfer. We examined this possibility by comparing the strategies for the optimal areas obtained for  $Z_1/Z_2 = 0.5$  and  $2.0$  with the strategies for the corresponding areas when  $Z_1/Z_2 = 1$ . These results are shown in Fig. 1(b) and it shows that changing the area without any change in food quality also result in

a change in vigilance behaviour similar to that obtained in Fig. 1(a). However the arrangement of birds between the inner and outer regions is very different. Therefore we conclude that altering the ratio  $Z_1/Z_2$  has a large effect on the arrangement of birds but that the increase in the proportion of time spent feeding is mainly due to the smaller areas.

If it is true that the inner region has a better food source, then we might expect that this is only the case for a certain area, and that if the flock size increased, then only a part of the inner region would have the better food source. Or if the flock was very small, then some of the outer birds might benefit from a better food source in part of their region. In the next section, we investigate this possibility.

2.2.2. A fixed area has a better food source

We assume that the total available feeding area has an inner region of size  $x \text{ m}^2$  which has a better food source than the rest of the region. We introduce two new parameters to represent the quality of the food source,  $V_1$  for this inner region, and  $V_2$  for the rest of the area, where  $V_1 \leq V_2$ . The area occupied by the inner birds,  $A_1$ , may be greater than, less than or equal to  $x$ .

If  $A_1 > x$ , then

$$Z_1 = \frac{xV_1 + (A_1 - x)V_2}{A_1}, \quad Z_2 = V_2.$$

If  $A_1 \leq x$ , then

$$Z_1 = V_1, \quad Z_2 = \frac{(x - A_1)V_1 + (A_2 + A_1 - x)V_2}{A_2}.$$

We let  $V_1 = 0.5$  and  $V_2 = 1$ , which corresponds to the inner  $x \text{ m}^2$  being twice as good as the rest of the feeding area. We chose  $x = 4, 8, 16$ . The results are shown in Fig. 2 below. The model predicts that as  $x$  increases then the payoffs increase, which is to be expected. If  $x = 8$ , then the predictions are almost identical to the case where  $Z_1/Z_2 = 0.5$  (see Fig. 1(a)), since the best inner area in these cases is  $7 \text{ m}^2$  and so the outer birds are not going to benefit noticeably. If  $x = 4$ , then the inner

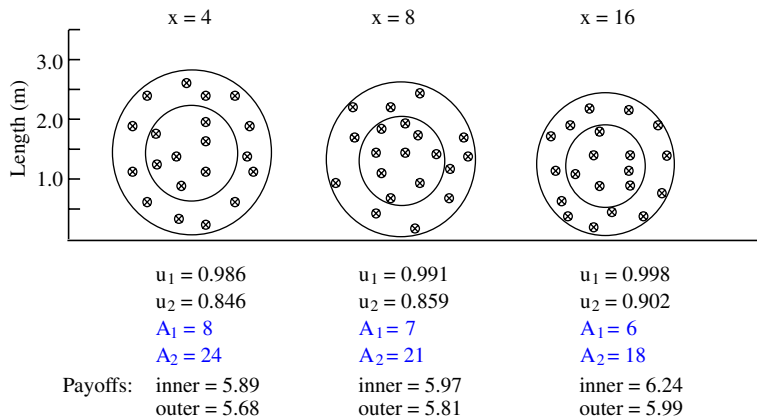


Fig. 2. How the strategy for the proportion of time spent feeding ( $u_1, u_2$ ), area ( $A_1, A_2$ ) and arrangement of birds ( $N_1, N_2$ ) changes when the fixed inner area,  $x$ , has a better food source.

region is not so good and so it is best for slightly more birds to go into the outer region. When  $x = 16$ , the model predicts that it is best for the birds to move closer together with the inner birds spending nearly all their time feeding and doing better than the outer birds. There is also the possibility that  $A_1 + A_2 < x$ , for large  $x$ . In this case, all birds benefit from a better food source and our model predicts that birds will feed in smaller areas, increase their safety and so increase their payoffs (data not shown).

So far we have assumed that all birds are equally likely to be targeted by a predator. We would expect that the model predictions would be very different if this was not the case and so we consider this possibility in the next section.

### 2.2.3. Outer birds are more likely to be targeted

It may be reasonable to assume that birds in the outer region are more likely to be targeted by a predator than birds in the inner region. This would certainly be true if we were considering a ground predator, but studies have shown that this is also likely to be true for aerial predators (e.g. [27]). It has also been noted that dominant birds tend to feed in the centre where it is safer, while juveniles end up on the edges of flocks and are more often caught by predators [19].

The results for  $\tau = 1, 1.5$  and  $2$  are shown in Fig. 3. As  $\tau$  increases from 1 to 1.5, the model predicts that the area and the arrangement of birds remains the same but the outer birds become more vigilant and receive a lower payoff. The inner birds benefit from the increased vigilance of the outer birds and can now spend more time feeding and receive a higher payoff. When  $\tau$  increases from 1.5 to 2, the model predicts that all the birds increase their safety by moving closer together and this results in all birds being able to spend more time feeding and so increase their payoffs. It may seem counter-intuitive that outer birds do better when their relative risk becomes greater. However, the outer birds only receive a very small increase in their payoff and this could be due to the fact that we only allowed discrete areas in our model, whereas the true optimal areas are probably somewhere in between. The model predicts that the inner group does better if the outer birds are preferentially targeted. Our model predictions explain why the inner group is more likely to be composed of dominant birds. At the ESS, no animal gains from unilaterally changing

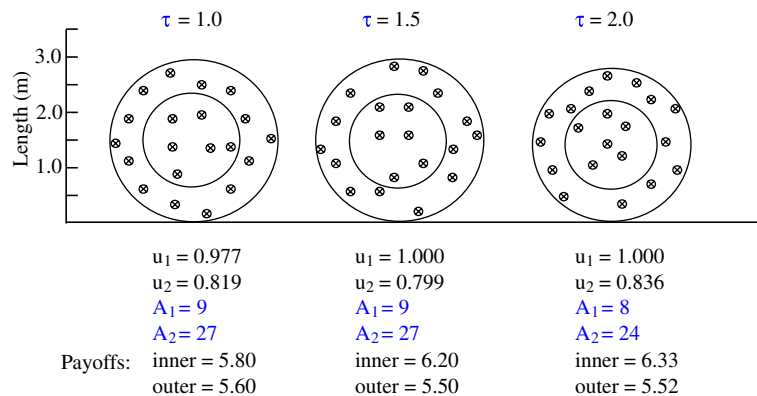


Fig. 3. How the strategy for the proportion of time spent feeding ( $u_1, u_2$ ), area ( $A_1, A_2$ ) and arrangement of birds ( $N_1, N_2$ ) changes with the relative risk of attack,  $\tau$ .

location, but an individual in the outer region could gain by exchanging places with a bird in the centre. This could happen if a dominant outer bird forced a subordinate inner bird to exchange places. In this way, we would expect all the dominant birds to end up in the centre of the group.

#### 2.2.4. Varying flock size

For a flock size of 20 birds, we assumed that the outer region was three times larger than the inner region. However, as flock size increases and hence the area increases, this assumption may no longer be valid. We will now assume that the width of the outer region can be no more than 2 m. If the radius of the inner circle is less than 2 m, then the width of the outer region is equal to the radius of the inner circle and the outer area is three times larger than the inner region. This will be true when the total area is about 50 m<sup>2</sup>, with an inner area of 12.5 m<sup>2</sup> and an outer area of 37.5 m<sup>2</sup>. For larger total areas, we first calculate the inner radius and hence the inner area, and then finally the outer area. Note that these calculations will result in inner and outer areas which are not integer values, although the sum of the two areas will be an integer. In each case, the inner and outer areas are rounded to the nearest quarter of a metre. The smallest flock we consider is 10 birds, as otherwise we could not clearly have an inner and outer group.

Table 2 shows the model predictions for when the flock size is 10, 20, 30 and 50. We find that birds in flocks of size 10 receive an average higher payoff per bird. As the flock size increases, the average individual payoff decreases. The reason for this result is that larger flocks require larger areas and one of the assumptions of our model is that communication is poorer in larger areas, so that large flocks do not benefit from an increase in safety. This may not necessarily be the case, for example, an individual may obtain information about a predator from another individual that is close by and then pass on the information to other nearby neighbours [8]. We modified our model to let the probability  $P_A$  depend on the density of birds rather than the area. In this case our model predicts that the vigilance of outer birds decreases with flock size (with no significant change in the vigilance behaviour of inner birds) and that large flocks do better as they are able to feed in larger areas without compromising their safety (see [8]). However, larger groups and larger areas would probably attract more predators.

We also calculated the total vigilance of the flock to see whether or not this declines with group size. Following Lazarus [15], if  $Q$  is the proportion of individuals in the inner group, so that  $1 - Q$  is the proportion of individuals in the outer group, then total vigilance  $V$  is given by  $V = (1 - u_1)Q + (1 - u_2)(1 - Q)$ . The values of  $V$  for flock sizes 10, 20, 30 and 50 were 0.1344, 0.1336, 0.1431 and 0.1701, respectively. Thus initially total vigilance declines as flock size increases from 10 to 20, but then increases for larger flock sizes. Large flocks mean large areas and the probability of being informed decreases, and so individuals have to be more vigilant. This prediction is

Table 2  
Varying the flock size

Flock size	$A_1$	$A_2$	$N_1$	$N_2$	$u_1$	$u_2$	Inner payoff	Outer payoff	Total payoff
10	5.0	15.0	3	7	1.000	0.808	6.24	5.62	58.12
20	9.0	27.0	6	14	0.977	0.819	5.80	5.60	113.22
30	12.0	36.0	8	22	0.983	0.811	5.82	5.32	163.54
50	29.0	51.0	22	28	0.971	0.719	5.22	5.04	255.95

in contrast with the widely reported phenomena of declining vigilance with flock size [28–30]. However, these studies were mostly for small groups; for example Elgar and Caterall found no appreciable decrease in vigilance rates with flock size for groups larger than five [30]. In our model, we did in fact find a decline in vigilance rate with flock size for small groups (up to 20 birds), so our models do agree with experimental data. These findings suggest that birds may only be able to get information from near neighbours so that in effect, vigilance behaviour is only affected by the number of near neighbours (which would probably not be greater than five). However, large groups would benefit from the dilution effect, although they may also attract more predators [31,32].

As the flock size increases, our model predicts that the average flock density increases initially but levels off once flocks reach about 50. In all cases, the flock density is higher for the inner birds and the inner birds continue to move closer together up to flock size of 50. However, for the outer birds, flock density initially increases but then decreases as flock size changes from 30 to 50. The prediction that the outer birds begin to space out in larger flocks is due to the fact that the probability of being informed is now very small, and there is no advantage in feeding closer together. The area of the inner group is still small enough for them to gain reasonable information, but we would expect that once flock sizes increased still further, that they would also start to space out more.

Inglis and Lazarus [17] suggested that the decline in vigilance with increasing flock size, which has been so often observed, is a result of the edge birds being more vigilant than those in the centre, because as flock size increases the proportion of birds on the edge declines. Therefore we calculated the proportion of edge birds for different flock sizes as predicted by the model. The results show that the proportion of edge birds is fairly constant for flock sizes of 10–30 with about 70% of birds being on the edge. This then declines so that there is 56% on the edge for a flock of 50 and just 30% for a flock of 100. There was no decline for smaller flock sizes due to the fact that we allowed the outer area to be three times larger than the inner area until the total area was greater than 50 m<sup>2</sup>. The models predict that for flock sizes that required areas smaller than this the birds were divided between the inner and outer areas in ratios of about 3:7.

### 2.2.5. Varying the attack rate

We would expect that the birds' strategies would be sensitive to the predator attack rate and so we vary this parameter to see how the model predictions are affected. These results are shown in Table 3. The model predicts that the birds respond by either reducing the area or by increasing their vigilance, or both. As expected, the payoffs decline as the attack rate increases.

Table 3  
Varying the attack rate

$y$	$A_1$	$A_2$	$N_1$	$N_2$	$u_1$	$u_2$	Inner payoff	Outer payoff	Total payoff
0.000010	12	36	6	14	0.993	0.935	6.43	6.32	127.01
0.000025	9	27	5	15	0.990	0.885	6.29	5.83	118.86
0.000050	9	27	5	15	0.982	0.826	6.25	5.55	114.55
0.000075	8	24	5	15	0.985	0.833	6.03	5.37	110.61
0.000100	9	27	6	14	0.968	0.745	5.76	5.28	108.50

Table 4  
Varying the attack rate when inner group is safer ( $\tau = 2$ )

$y$	$A_1$	$A_2$	$N_1$	$N_2$	$u_1$	$u_2$	Inner payoff	Outer payoff	Total payoff
0.000010	9	27	6	14	1.00	0.945	7.17	6.19	129.62
0.000025	8	24	6	14	1.00	0.887	6.41	5.76	119.09
0.000050	8	24	6	14	1.00	0.836	6.33	5.52	115.25
0.000075	8	24	6	14	1.00	0.805	6.25	5.38	112.78
0.000100	8	24	6	14	1.00	0.782	6.19	5.27	110.91

2.2.6. Varying the attack rate when the centre of the group is safer

When we varied the attack rate in the previous section, we assumed that all birds had an equal chance of being targeted, i.e.  $\tau = 1$ . If birds in the outer group are more likely to be targeted, then a change in the attack rate may not affect the inner and outer groups in the same way. Therefore, we also vary the attack rate when  $\tau = 2$ , i.e. an individual in the outer region is twice as likely to be targeted as an individual in the inner region. The results are shown in Table 4. In this case, the inner birds spend all their time feeding for all the attack rates considered, and the outer birds increase their vigilance as the attack rate increases.

2.2.7. The centre group is safer but has less food

Some studies have suggested that the centre of the group is safer but that food is more abundant at the edge of the flock e.g. [25]. This can be easily modelled by setting  $\tau = 2$ , so that the outer birds are twice as likely to be targeted by a predator, and setting  $Z_1/Z_2 = 2$ , so that the outer region has twice as much food available as the inner region. The predictions are shown in the first column of Fig. 4. The second column shows the predictions for the model in which predation risk is higher for the outer group but food availability is the same for all. The third column shows the predictions for the default model in which predation risk and food is the same for everyone. By

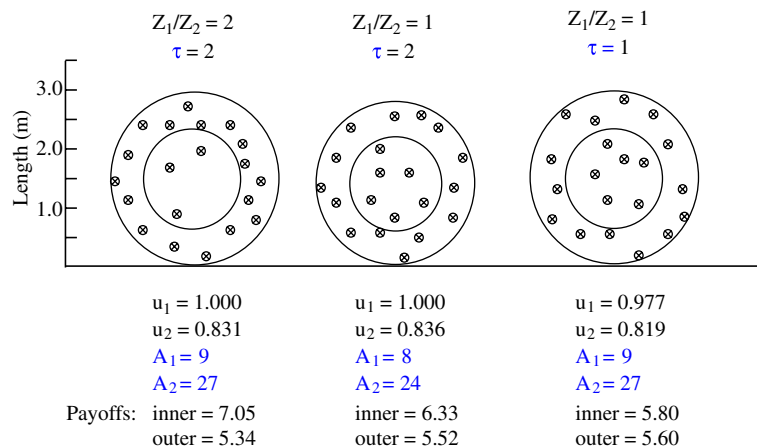


Fig. 4. How the strategy for the proportion of time spent feeding ( $u_1, u_2$ ), area ( $A_1, A_2$ ) and arrangement of birds ( $N_1, N_2$ ) changes when the inner group is safer but has a poorer food source.

comparing the models we can see that there are fewer birds in the centre when the centre is safer but has less food. This is probably due to the inner birds requiring more space to make up for less food. The inner birds feed all the time and each individual in the centre does better at the expense of the outer birds. Although the outer birds have a better food source, they have less space in which to feed and they have to be more vigilant. This model would be applicable if dominant birds position themselves in the safer centre of the group, forcing subordinate birds to feed on the edge, as suggested by some studies (e.g. [19]).

### 3. Discussion

In this paper, we modified our previous spatial models of vigilance in order to examine the possibility of the ‘edge’ effect. We divided the feeding area into an inner and outer region and allowed certain parameters of the model to depend on these positions. For a given sized flock, we found the best arrangement of birds between the inner and outer regions. Our models predict that the outer birds are always more vigilant than the inner birds. If the inner and outer groups were the same in respect to food availability, predation risk, and information transfer, then predictions were almost identical to those of Proctor et al. [8], so that there was no position effect. It seems plausible that the inner birds are more likely to receive information about a predator than outer birds, due to the fact that they have a better view of other members of the flock. This was the first position effect that we modelled and in this case our models predicted that the inner birds received a higher individual payoff, due to the fact that they spent more time feeding than the outer birds, and could benefit from the outer birds’ vigilance.

It has been suggested that predation risk is greater for birds on the edge of the group, and also that more food may be available on the edge. Another possibility is that the food source may be better in the centre of the group where the flock initially starts to feed before other individuals join and enlarge the flock. Therefore, we investigated these effects by varying the relevant parameters in the model. If predation risk is greater for the edge birds, then our model predicts that the outer birds increase their vigilance, and so do less well. The inner birds are able to feed more, as they take advantage of the vigilance of the outer birds and the fact that they are less likely to be targeted by a predator. If the outer region has a better food source, at the same time as being less safe from predators, then our model predicts that more birds feed in the outer region, and flock density increases at the edge, and so they do even worse than before. On the other hand, the inner birds are doing better, although there are now fewer of them. The situation of a safer centre region but with less food available, would make sense if the inner birds were a dominant group that were spacing themselves out and not allowing any of the subordinates to come into their feeding space.

In most circumstances, our models predict that flock density is not the same for the inner and outer groups. An important factor affecting flock density is the amount of food available, with the group with the most food available feeding at higher density. Predation risk also affected flock density, with birds in both groups feeding at higher densities if predation risk increased for the outer group. As flock size increases, our models predict that flock density increases for the inner birds, but for the outer birds flock density only increases up to a flock size of about 30 and then decreases again. This was explained by noting that once areas become large, the probability of being informed of an attack becomes very small and so the advantage of increasing the area to



increase food availability outweighs any advantage of feeding closer together. At a flock size of 50, the inner birds still have a reasonable chance of being informed, but we would expect that they would also eventually start to spread out as flock size increases. Our predictions about heterogeneity in density within flocks invite empirical testing.

Our models predicted that vigilance increases with flock size for large flocks (greater than 20) but we noted that for small flock sizes, vigilance does decline with flock size in agreement with empirical studies. The reasons for these results is that for large flock sizes, the probability of information transfer is small and so it is best for individuals to increase their own vigilance. Our models support the hypothesis that only near neighbours make good vigilance mates [13].

There are a number of factors that we have not dealt with, or have considered in a simplified way, in this paper, as our main priority was examining the edge effect. For example, we did not consider the shape of the flock, but this certainly would affect a number of factors, not least the proportion of centre to edge birds. For simplicity, we only considered two spatial groups: an inner and an outer group. Our model could be extended to allow for a variety of positions by either considering the distance from the most central point of the group, or by considering distances to neighbours. We would not expect the results of a model considering distances to neighbours to be very different to the results obtained for the model presented here, since as noted in the previous paragraph, only near neighbours make good vigilance mates.

An interesting approach would be to use a more explicit spatial arrangement of birds, as proposed by James et al. [24]. They introduced the concept of an individual's 'limited domain of danger' (a modification of Hamilton's 'domain of danger' [7]), whereby the domain of danger is bound by a circle of radius  $r$ , but in which the area is reduced by any bisector generated by a neighbouring animal which is closer than a distance of  $2r$ . Using this simple geometrical construct, James et al. [24] were able to analyse the predation risk of both peripheral and central individuals in a group. Future work combining this explicit spatial approach with the model in this paper may prove very fruitful.

In our models, we assumed that the flock of feeding birds was stationary. It would be interesting to modify our model to allow for mobile groups; in this case we would need to consider the difference between 'back' and 'front' individuals [33]. Another aspect which could be investigated further, is allowing the proportion of the inner to the outer area to vary, as in this paper we chose a rather arbitrary definition.

The models in this paper have been motivated by studies which have shown that birds on the edge of a group are more vigilant than those in the centre. By considering a flock of birds divided into an inner and outer group, we have been able to examine what happens when different factors affect these two groups. Two main predictions emerge. Firstly, outside birds have to be more vigilant than inner birds, and secondly the reward to inner birds is greater, making the centre attractive to dominant individuals. Both are in accord with empirical evidence.

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## Appendix A. Finding the best arrangement of birds

First we made an initial guess for the total area and chose an arrangement of birds between the inner and outer regions. For this arrangement we found the pair  $(u_1, u_2)$  to give the ESS and calculated the payoffs. We then repeated the procedure for all allowable arrangements of birds to find the stable solution (e.g. if inner payoff for arrangement  $(N_1 = 4, N_2 = 16) >$  outer payoff for arrangement  $(N_1 = 3, N_2 = 17)$  then the outer bird in arrangement  $(N_1 = 3, N_2 = 17)$  should move to the inner region, and arrangement  $(N_1 = 3, N_2 = 17)$  would not be stable. Similarly, we checked to see if an inner bird should move). Fig. 5 shows how the payoffs change for the inner and outer individuals as they change groups. For example, we can see that if there are four birds in the inner group, then an outer individual can improve its payoff by changing groups (see dashed line in figure). Conversely if there are six inner birds, an inner bird can do better by moving into the outer group. Therefore, we obtained a stable arrangement of 5 inner and 15 outer birds for the chosen area. We then repeated the whole procedure over a range of areas and found the area which maximises the total payoff for the group.

It should be noted that the optimal area for the whole group may not give the optimal area for all individuals in the group. In general, we obtained an optimal area that is either best for the inner group or the outer group but not both groups simultaneously (see Table 1). This is not ideal. However, the optimal areas for each group were always close (e.g. for the default parameters, area  $(A_1 = 8, A_2 = 24)$  was best for the inner group and area  $(A_1 = 9, A_2 = 27)$  was best for the outer group).

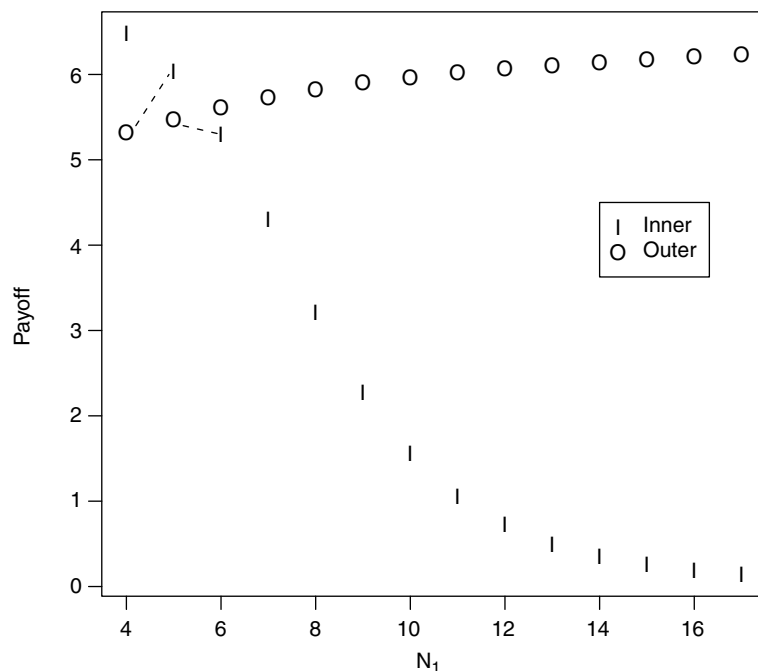


Fig. 5. How the payoffs to individuals in the inner and outer group change as the number of birds in the inner region ( $N_1$ ) varies.

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