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A Communication-Based Spatial Model of Antipredator Vigilance

CAROLE J. PROCTOR*†, MARK BROOM‡§ AND GRAEME D. RUXTON‖

†*Department of Gerontology, University of Newcastle, Institute for Ageing and Health, Newcastle General Hospital, Newcastle upon Tyne, NE4 6BE, U.K.* ‡*Centre for Statistics and Stochastic Modelling, School of Mathematical Sciences, University of Sussex, Falmer, Brighton, BN1 9QH, U.K. and* ‖*Division of Environmental and Evolutionary Biology, Institute of Biological and Life Sciences, University of Glasgow, Glasgow, G12 8QQ, U.K.*

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Many animals spend their lives performing two often mutually exclusive tasks: feeding and watching out for predators (anti-predator vigilance). There have been many theoretical and empirical studies investigating this trade-off, especially for birds. An important characteristic of a flock of real birds is the area occupied by the flock. Individuals feeding close together experience increased competition so that the feeding rate decreases. Widely spaced individuals may suffer a loss in vigilance efficiency, since communication between individuals is more difficult, such that the predation risk increases. A vigilance model is developed which allows birds to control their spacing (and so the area of the flock) as well as their vigilance rate. The best strategy for the birds is found under a variety of environmental conditions, under the assumption that each individual acts selfishly to maximize its own fitness.

1. Introduction

1.1. ANTIPREDATOR VIGILANCE

The lives of many animal species are principally divided between foraging for food, and avoiding predation by other animals. These activities are often mutually exclusive, so that extra effort in one reduces the effort available to the other. Thus when an animal forages for food, it must divide its time between feeding and being vigilant for predators. Many animals, especially birds, form groups to feed, and it has been observed that there is an inverse relationship between individual vigilance and group size. This can be explained by two separate effects.

(1) *The group vigilance hypothesis*: When an individual detects a predator, this information may be passed to its group mates either through an alarm call or sudden flight (Davis, 1975; Lazarus, 1979; Pulliam, 1973).

(2) *The individual risk hypothesis*: Members of the flock benefit from the "dilution" effect. The larger the group, the less likely a particular animal is to be killed (Dehn, 1990; Hamilton, 1971).

The combination of these two effects makes group feeding especially beneficial (Dehn, 1990; Roberts, 1996) and the time saved through reduced vigilance can thus be devoted to foraging (or other activities).

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*Corresponding author. Tel.: +44 (0)191 256 3391; fax: +44 (0)191 219 5074.

§M. Broom is also a member of the Centre for the Study of Evolution at the University of Sussex.

E-mail addresses: c.j.proctor@ncl.ac.uk (C.J. Proctor), m.broom@sussex.ac.uk (M. Broom), g.ruxton@bio.gla.ac.uk (G.D. Ruxton).

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We have assumed here that food gathering and anti-predatory vigilance are mutually incompatible activities. However, recent empirical evidence (Robinette & Ha, 2001) and theory (Beauchamp, 1998) suggest that scanning in birds may serve the dual function of anti-predatory vigilance and seeking opportunities to exploit food discoveries by other group members. Such a situation would make considerable changes to the predictions of our model. In particular, we might not predict that vigilance rates decline with group size. Further work (both empirical and theoretical) of this idea would be of interest.

The tendency of birds to forage in groups has produced a large body of theory (for example, Broom & Ruxton, 1998; Lima, 1987; McNamara & Houston, 1992; Pulliam *et al.*, 1982). Proctor & Broom (2000) developed a model that introduced the idea of the area used by the flock as a strategic variable under natural selection. Under the model, there is always an optimal combination of flock area and vigilance level, which depends upon the environmental parameters chosen. The optimal area is hardly affected at all by some factors, such as the ability to spot predators, although this has a large effect upon the vigilance level. Other parameters, such as food density, affect the area greatly. A key assumption of this previous model was that it took longer for individuals to scan for predators if they were feeding in large areas as they had a wider region to survey. It was assumed that the length of a vigilance scan increased as the area used by the flock increased, being proportional to the length of the perimeter of this region. Whilst this is plausible under certain circumstances (Bahr & Bekoff, 1999), it is not in others (Lima & Bednekoff, 1999) where attacks come from only a single direction. However, there is likely to be another cost to being spread out over a large area, namely poor communication between individuals of imminent attack. Pöysä (1994) and Blumstein *et al.* (2001) found that near individuals make better vigilance mates. In this paper we explore the consequences of such a cost.

1.2. SPATIAL FACTORS

Consider a flock of 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 utilizing large and small areas. If the area is small, there will be less food available and so food gains will be small; however, individuals will be closer together and therefore safer from predators, because warnings will be easier to detect (Pöysä, 1994). This particularly applies when warnings are the sudden flight of one or more birds, rather than alarm calls. Another advantage of having dense flocks is that they can confuse predators during an alarm flight. Flocks are known to reduce their spacing due to the appearance of predators (e.g. Caraco, 1979). Although birds cannot pick the area of the flock per se, it is reasonable to suppose that individuals can adjust their neighbour distance, which would have an effect on the flock area. Some studies found an inverse relationship between flock size and neighbour distance (Williamson & Gray, 1975; Patterson *et al.*, 1971). However, both of the cited studies found that the relationship was also linked to season. Rolando *et al.* (2001) found that there was no significant correlation between flock size and neighbour distance in a study of red-billed choughs, *Pyrrhocorax pyrrhocorax,* but they found a positive correlation between vigilance and neighbour distance; this was only true for distances of 3–6 m, with no apparent increase in vigilance for distances of 6–10 m.

The shape of the region occupied by a flock is also of interest. This will depend on the type of habitat and the presence of any obstructions or boundaries. For instance, a flock feeding in a field may be expected to form roughly circular groups, whilst a flock of waders on the seashore will tend to form long elliptical groups. Bekoff (1995) studied the effect of the geometric arrangement of western evening grosbeak, *Coccothraustes vespertinus*, on vigilance behaviour. He found that individual grosbeaks arranged in linear arrays of three or more birds are more vigilant than birds arranged in circular groups.

Unlike Pulliam (1973), we will not assume that if one bird spots the predator then the rest of the group is also informed and all escape. Instead we will assume that any individual which spots the predator will pass on the information to another *particular* individual with a probability P_A, and that this probability will decrease as the area increases.

2. The Model

We assume that the predator targets a particular individual, with each individual having the same probability of being chosen. The predator requires a certain time for its 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. It will be spotted by any individual in the flock that scans during this interval, scans being of length t_s. For the probability that an individual does not spot the predator, denoted by P_{ns}, we follow Pulliam *et al.* (1982)

$$P_{ns} = u\mathrm{e}^{-b((1/u)-1)}, \tag{1}$$

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

If one individual spots the predator, then the probability that another is informed of the attack before time t_a is a decreasing function of the area occupied by the flock (A), for a given flock size. Any particular individual may itself spot the predator with probability $P = 1 - P_{ns}$, or may be informed of an attack by each member of the flock with probability PP_A.

We assume that any bird, which spots the predator, gives a warning by taking flight suddenly, i.e. without any pre-flight movements. An individual is more likely to obtain information from another individual that is close by, and it is then likely to pass on the information to other individuals that are close to it. This process would rapidly continue until the whole flock is notified of the attack (for the consequences of when this knock on effect is assumed not to occur, for example if an attack occurs very quickly, see Proctor, 2000). This means that P_A should be an increasing function of the number of birds in the flock, N, for a given flock area. If another bird spots the predator, then there are $N-1$ other birds that it can inform. If it informs just one other bird then this individual may pass on the information and the process cascades until our particular individual is informed. Thus P_A is a function of the density of the (other) birds within the area. We define P_A as follows:

$$P_A = \frac{1}{1 + \left(9\gamma A/(N-1)\right)^d}, \tag{2}$$

where γ and d are positive real numbers. The factor 9 is included for convenience; under the default parameters $P_A = 0.5$ when $A = 1/\gamma$. γ may be interpreted as a measure of the ability to communicate for a particular shaped area. In our model we assume that the feeding area is circular so that decreasing γ results in better communication between birds. Figure 1 shows how for a constant area of 20 m^2, P_A increases as N increases.

We should note that for simplicity we have ignored the effect of position within the group. We would expect that birds within the centre of the group would learn more from others than those on the periphery, which are more isolated. The effect of position is explored in detail and modelled in Proctor 2000.

In our model, the cost of feeding is the product of the attack rate, the cost of being targeted and being unaware of the attack, and the probability that the targeted bird is unaware of the predator P_{tu}. The latter probability is the product of the probability that an individual does not spot the predator and the probability that the individual is also not informed by any other member of the group. The first term is simply $P_{ns} = (1-P)$; the second term is $(1-PP_A)^{N-1}$, assuming that each individual

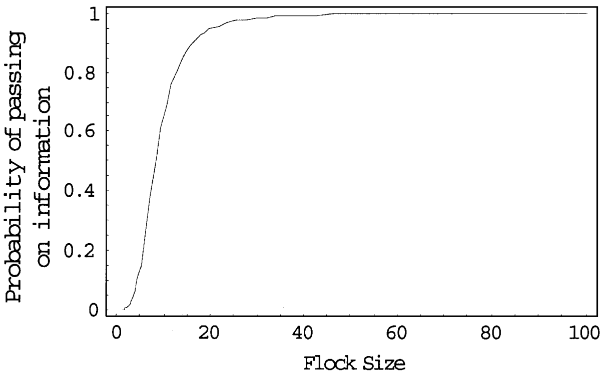

FIG. 1. How the probability of passing on information changes with flock size for a fixed area. Here area for the group, $A = 20$ and information parameter, $\gamma = 0.04$.

scans independently of all others, so that

$$P_{tu} = (1 - P)(1 - PP_A)^{N-1}. \qquad (3)$$

Note that there are other costs of feeding, for instance the time wasted and energy expended caused by a disturbance that is not the result of a predator attack or the cost due to predation risk when the birds are not feeding. These are not considered for reasons of simplicity; it is likely that these costs are effectively independent of the strategies adopted by the birds, and so should not affect the choices that they make. In this paper it will be assumed that individuals behave selfishly as regards vigilance behaviour, as this strategy is evolutionarily stable (Maynard Smith & Price, 1973). This means that birds scan at the rate for which any deviating individual has a lower fitness and so "cheating" does not pay. However, data has shown that birds scan at higher rates than a selfish optimum would predict (Pulliam *et al.*, 1982). Therefore, we also consider finding the cooperative optimum and show how this compares with the selfish optimum in Section 5.

The payoff function for this model is based on that of Broom & Ruxton (1998) and Proctor & Broom (2000). There are different models, which use different functions to optimize the balance between feeding and vigilance. Many use survival as the measure and assume that the cost of lowered vigilance is an increased risk in mortality. In this paper, we model this cost as an energetic penalty (see Appendix A for an explanation). There are a variety of ways of constructing a payoff function, depending upon circumstances, and since our main aim is to concentrate on the spatial effects, we have chosen a relatively simple one, incorporating the major factors.

We will use the approach of McNamara & Houston (1992) and consider the behaviour of a "mutant" individual which spends a proportion of time u feeding when other group members spend a proportion of time v. We assume that the area of the flock is determined by individual decisions about spacing but that each individual does not choose a different spacing to everyone else. In other words, we assume that all birds within a flock will adjust their spacing simultaneously, e.g. all move closer together if danger threatens. The mutant's best response is to feed for a proportion of time u that maximises the payoff function for this individual. The payoff for the mutant is

$$F_v(u) = \left(1 - \frac{1}{1 + (A/NZ)^m}\right)\theta u - yK\frac{1}{N}(1 - P)(1 - QP_A)^{N-1}. \qquad (4)$$

The first term in brackets on the right-hand side of eqn (4) represents the rate of food uptake which depends on the area, A, the flock size, N, and the area that a bird requires to feed at half its capacity, Z, (see Proctor & Broom, 2000, for its derivation), and m, a measure of how fast feeding rate increases with area. This function was chosen so that the feeding rate is an increasing function of A, but that the rate of increase slows down as A becomes large and eventually reaches an asymptote. The feeding rate also decreases with the number of foragers per unit area. This is due to competition for the same food source. Note that if food is abundant then this corresponds to a very low value of Z, so that there will be little interference from other foragers. θ is the maximum feeding rate, y is the predator attack rate per second, K is the cost (in Joules) of an attack [the amount of energy lost if a bird is attacked and killed—see Proctor & Broom (2000) for more details] and $Q = 1 - ve^{-b((1/v)-1)}$, which is the probability that any other group member spots the predator. [Note that in eqn (4), P is the probability that the "mutant" individual spots the predator].

To maximize $F_v(u)$ we differentiate eqn (4) with respect to u and set equal to zero, giving

$$F'_v = \left(1 - \frac{1}{1 + (A/NZ)^m}\right)\theta + \frac{1}{N}yKP'(1 - QP_A)^{N-1}$$

$$= \left(1 - \frac{1}{1+(A/NZ)^m}\right)\theta - \frac{1}{N} yK(1-QP_A)^{N-1} e^{-b((1/u)-1)}\left(\frac{b}{u}+1\right) = 0. \quad (5)$$

At the ESS if the group is feeding for a proportion of time u^*, then the mutant's best response is also to feed for a proportion of time u^*. So we have

$$F'_{u^*}(u^*) = \left(1 - \frac{1}{1+(A/NZ)^m}\right)\theta - \frac{1}{N} yK(1-PP_A)^{N-1} e^{-b((1/u^*)-1)} \times \left(\frac{b}{u^*}+1\right) = 0. \quad (6)$$

where $P = 1 - u^* e^{-b((1/u^*)-1)}$.

Rearranging eqn (6), we obtain

$$\frac{\theta}{yK} = \frac{1+(A/NZ)^m}{N(A/NZ)^m}(1-PP_A)^{N-1} e^{-b((1/u^*)-1)}\left(\frac{b}{u^*}+1\right). \quad (7)$$

The optimal pair (u,A) was found by finding the optimal u for each A and then maximising over A.

Our model maximizes a function that is a linear relationship between food consumption and predation risk. In reality, birds will need a certain amount of food to survive per day, and there is a limited amount of food that they can use. Our model describes what happens when the birds are feeding in the open. Thus if food is plentiful, they may feed as rapidly as possible up to their physiological gut capacity, and then go to cover, so exposing themselves to risk for a short period only. If food is rare they may have to spend a great deal of time reaching the level that they need. This possibility is explored in our model by varying the parameter Z, which is measure of food availability (see Section 4.3.2).

3. The Model Parameters

Most of the model parameters are the same as those used in our previous model and have already been discussed in detail (Proctor & Broom, 2000). We chose default values based on empirical data and again detail is to be found in Proctor & Broom (2000). Here, we describe only the parameters that are new to this model.

3.1. THE PROBABILITY OF PASSING ON INFORMATION ABOUT A PREDATOR, P_A

We need to estimate d and γ. Due to a lack of appropriate data, the choice of d was necessarily rather arbitrary. Figure 2 shows a plot of P_A against A for $d = 1, 2, 3, 4$ for $\gamma = 0.04$, our eventual choice. $d = 3$ seemed to give a plausible shape to the graph. [However, it turns out that

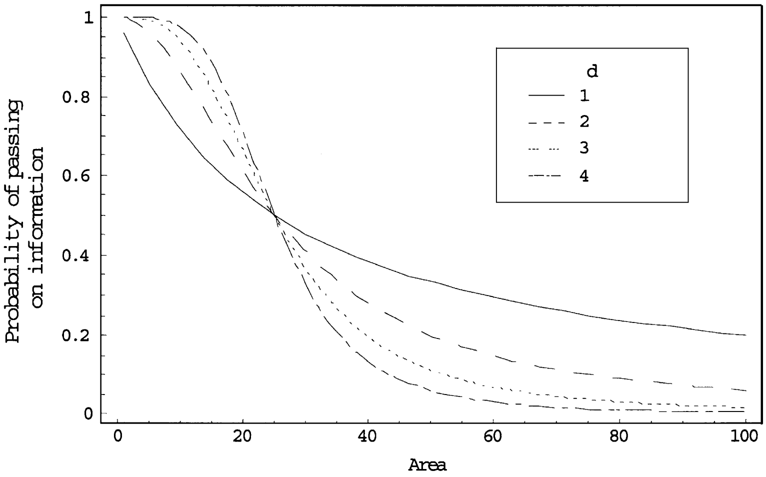

FIG. 2. The probability of being informed of a predator as a function of area for different values of the constant d.

the model is very robust to changes in d, see Proctor (2000)].

Hilton *et al.* (1999) studied escape flights of flocks of redshanks from sparrowhawk attacks. On average, approximately 46% of individuals flew immediately after their neighbours took flight, indicating that the probability of warning a neighbouring bird directly and thus starting a chain reaction of flights is about 0.46. The average flock size was 24 and the groups covered an area of about 60 m^2. Thus,

$$0.46 = P_A = \frac{1}{1+\left(60\times 9\gamma/23\right)^3}.$$

This gives us an approximate value for γ of 0.04, so that $P_A = 0.5$ when $A = 25$.

3.2. THE PARAMETER B

b is the ratio of the time taken for the predator to attack, t_a, and the length of scan, t_s. The length of scan is generally taken to be one second (Pulliam *et al.*, 1982), and we have selected the attack time t_a to be two seconds, in accordance with Proctor & Broom (2000), (see also Lendrem, 1983).

Choice of the other model parameters and their default values again follows Proctor & Broom (2000). Table 1 summarizes all the parameters and chosen default values. Note that u and A are the parameters that we are trying to optimize, and so do not have default values.

4. Results

All payoffs are shown on a scale 0–10 J s^{-1}, where 10 J s^{-1} is the value of the theoretical maximum rate of energy gain, which is attained when birds feed constantly in the absence of predators.

4.1. A FIXED AREA

In this section, we find the best vigilance strategy for a group that is occupying a specified area. This is shown in Fig. 3. In very small areas there is little food, so that it is not worth feeding (i.e. u is low) — realistically the birds would just go elsewhere, of course. For medium-sized areas, there is a fair level of food and communication is good, thus the feeding level is high since birds can be relied upon to inform others of a predator. Large areas give poor communication, but not that much more food — it therefore pays to be more vigilant, and so u is lower.

4.2. THE DEFAULT PARAMETERS

Our model predicts that the optimal strategy for a flock of ten birds is that they should spend 86% of their time feeding and 14% of their time being vigilant. The best area for the group is 20.8 m^2 and each bird receives a payoff of

TABLE 1
The model parameters

Parameter	Description	Default value
u	Proportion of time feeding	—
A	Area of region occupied by group	—
N	Number of birds in the group	10
θ	Maximum feeding rate	10 J s^{-1}
K	Cost of an attack	10^7 J
y	Attack rate	5×10^{-5} s^{-1}
t_a	Time taken for an attack	2 s
t_s	Time taken for bird to scan for predators	1 s
b	t_a/t_s	2
Z	Area required for bird to feed at half its capacity	1 m^2
m	A measure of how fast feeding rate increases with area	5
γ	A measure of the ability to communicate	0.04
d	A measure of how information transfer decreases with area	3

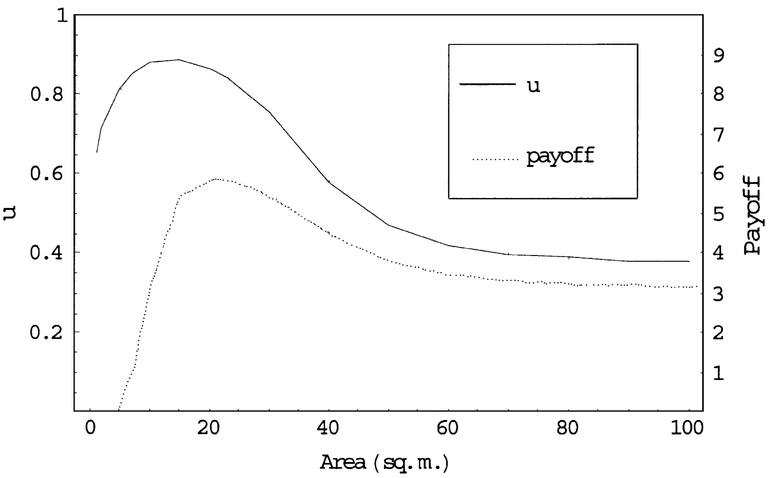

FIG. 3. The best strategy for the proportion of time feeding, *u* when the area is fixed. The value of *u* is indicated by the left-hand scale, the value of the payoff by the right-hand scale.

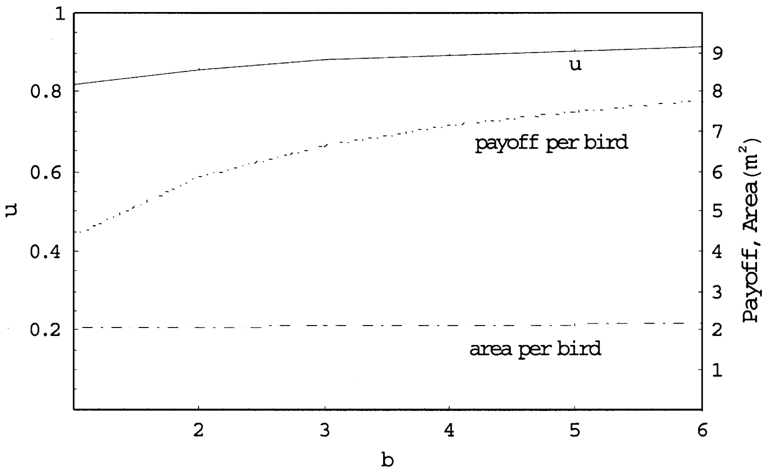

FIG. 4. How the strategy for the proportion of time feeding, *u* and the area changes with the ratio of the time taken for an attack and the time taken for a bird to scan, *b*. The value of *u* is indicated by the left-hand scale, the values of the payoff and the area by the right-hand scale.

$5.9\,\mathrm{J\,s^{-1}}$, which is 59% of the maximum possible payoff.

4.3. VARYING THE PARAMETERS

In the previous section we chose a set of "default" parameters that we considered reasonable. However, different parameters may prevail in reality either due to natural variation or to the inaccuracy of our choice. Therefore, the parameters were changed to see the effect upon model predictions. Each of the parameters was varied in turn, while the rest were kept at their default values in order to see how the model predictions were affected. Space does not permit the inclusion of the results for every variable (for a full discussion see Proctor, 2000). The results for the variables that are of particular interest are shown in the figures below.

4.3.1. *Varying the Ratio of Attack Time to Scan Time, B*

In our model *b* depends on the predator attack time and the time taken for a bird to make one scan. An increase in *b* can be interpreted as either an increase in the attack time or a decrease in the time taken for a scan. Figure 4 shows that as *b* increases, our model predicts that there is an increase in both *u* and the payoff, the area staying roughly the same. As *b* increases attacks are relatively slower, so the rate of vigilance does not need to be as high, so increasing the overall payoff.

4.3.2. *Varying the Area Required for a Bird to Feed at Half its Maximum Capacity Z*

Z is the area required per bird to feed at half its maximum feeding rate. So *Z* is a measure of the quality and/or density of the available food source. Figure 5 shows that our model predicts that as *Z* increases, *A* increases quite considerably. This is to be expected, since increasing *Z* means increasing the area required per bird. At the same time *u* decreases, since birds need to be more vigilant when the area increases, due to a decrease in the probability of being informed of an attack. This is in good agreement with the observational findings of Rolando *et al.* (2001). Due to the decrease in *u* the payoff also decreases. Low *Z* means that there is a lot of food available, so the birds only need to feed quickly for a short time and then go to cover. If *Z* is high then the relative predation risk is high, since birds are feeding further apart and communication is less effective, so they should be very vigilant but feed for a long period of time.

4.3.3. *Varying the Attack Rate, y*

Our model predicts that as the attack rate increases, birds become more vigilant and move closer together (see Fig. 6). These predictions agree well with observed data (e.g. Caraco, 1979). Yosef (1997) found that, when the rate of disturbance increases, flamingos move closer together but continue feeding. In other studies, birds stop feeding and move closer together during disturbance (e.g. Myers, 1984). So birds may seek companions through some sort of selfish herd effect. Our model indicates that communication effects on their own may be sufficient to drive changes in forager density.

4.3.4. *Varying the Communication Parameter, γ*

The value of γ corresponds to $P_A = 1/2$ if the area of the flock of birds is $1/\theta\,\mathrm{m}^2$, so that the lower γ is, the better the communication between the birds. Thus, if γ is small, the birds are relatively safe in a large area and so can spend more time feeding. Conversely, if γ is large, then the probability of being informed of an attack becomes very small if the area is large, and so the best strategy is to choose a smaller area and spend less time feeding in order to increase the chance of spotting a predator. Figure 7 shows that increasing γ results in both *u* and *A* decreasing. Note that the value of γ may depend

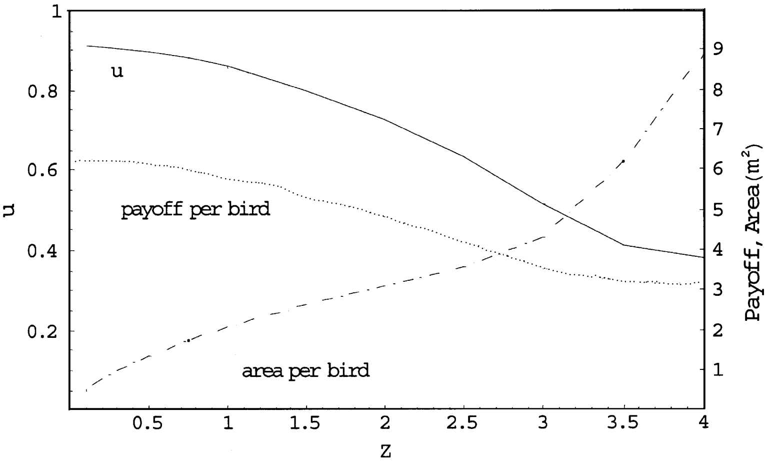

FIG. 5. How the strategy for the proportion of time feeding, *u* and the area changes with the area required for a bird to feed at half its capacity, *Z*. The value of *u* is indicated by the left-hand scale, the values of the payoff and the area by the right-hand scale.

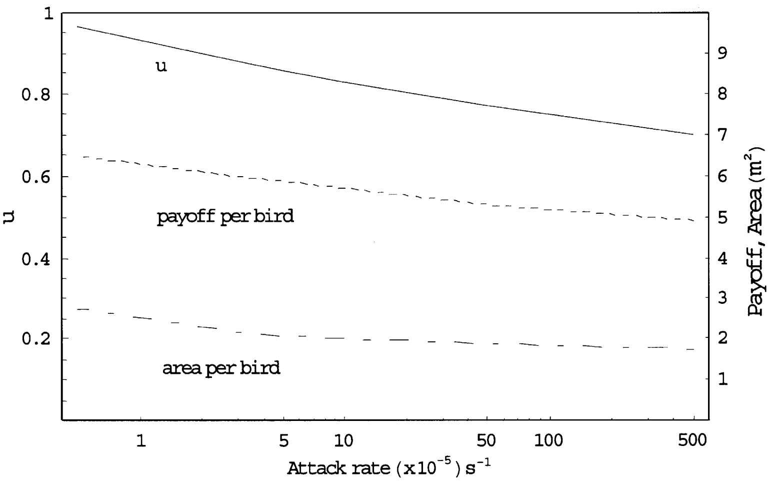

FIG. 6. How the strategy for the proportion of time feeding, *u* and the area changes with the attack rate, *y*. The value of *u* is indicated by the left-hand scale, the values of the payoff and the area by the right-hand scale.

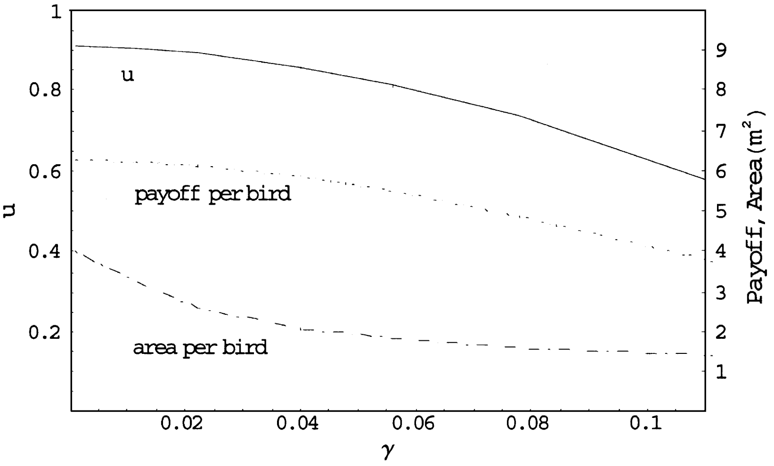

FIG. 7. How the strategy for the proportion of time feeding, *u* and the area changes with the ability to communicate $\tilde{a}$. The value of *u* is indicated by the left-hand scale, the values of the payoff and the area by the right-hand scale.

on the size of bird, and will also depend upon the shape of the feeding group and whether or not visual obstructions are present. It is easy to investigate the effect of shape since increasing the value of γ can also be interpreted as elongating the shape of the region. Our model predicts that birds in long thin regions feed closer together and are more vigilant that those feeding in circular regions which is in good agreement with the findings of Bekoff (1995). This would be due to individual birds having more near neighbours in circular groups.

4.3.5. *Varying Flock Size*, *N*

We now consider the most variable of the parameters, *N*, the number of birds. These results are shown in Fig. 8 (solid lines). As *N* increases, our model predicts that both *u* and the area per bird steadily increase. This means that vigilance declines with group size and the birds are benefiting by being in a larger group with the individual payoff increasing. Many studies have found that as group size increases, individual birds spend more time feeding and less time scanning (Caraco, 1979; Elgar & Caterall, 1981;

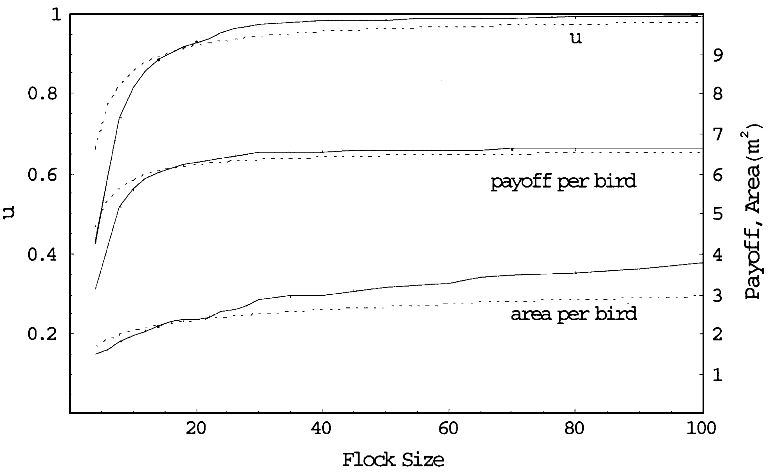

FIG. 8. How the strategy for the proportion of time feeding, u and the area changes with flock size, N, when the attack rate is independent of N (solid lines) or when the attack rate is proportional to N (dotted lines). The value of u is indicated by the left-hand scale, the values of the payoff and the area by the right-hand scale.

Elgar, 1989). The reason for this result is that, as flock size increases, P_A increases for a given flock area, and so we obtain larger areas for which the probability of passing on information about a predator is still high. The dilution effect will also have an important effect, as the risk of predation for any particular individual declines as group size increases. We investigated the relative importance of communication and the dilution effect by allowing the probability of being informed of an attack to be independent of group size. We found that communication was very important when group sizes are small but that the dilution effect was the dominating factor in large groups. The increase in both u and the payoff becomes very small when the flock size reaches about 30.

4.3.6. *Varying the Attack Rate with Flock Size*

So far we have assumed that the predator attack rate is constant for all group sizes. However, some studies have shown that predators are attracted to large groups as they are more easily located (e.g. Page & Whitacre, 1975; Sullivan, 1984). Therefore, we will now allow the attack rate to be proportional to N, with $y = 0.00005\,\mathrm{s}^{-1}$ when $N = 10$. So $y = 0.00005 \times N/10$. The dotted lines in Fig. 8 shows that our model predicts that the payoff initially increases, then levels off for N greater than 50. Although the attack rate is increasing with group size, the probability of being informed also increases with N and when flocks are large there is a high probability that at least one bird will spot the predator and pass on the information. Individuals spend slightly more time being vigilant than in the model where attack rate is independent of flock size, due to the greater risk of an attack. The model predicts that the area per bird increases with group size for small and medium-sized flocks (10–75 birds) but levels off for larger flocks. Also birds in large flocks feed much closer together than in the situation when the attack rate is independent of flock size (compare bottom lines in Fig. 8). Large groups are as safe as small groups despite the increase in attacks with flock size and so individuals can space themselves out and increase their food intake. In general, the pattern is very similar to when the attack rate was independent of group size, the main difference being in the spacing of the birds, especially in large groups.

5. Cooperative or Selfish Behaviour?

In an early theoretical explanation Pulliam *et al.* (1982) sought the vigilance rate that maximizes the probability of avoiding either predation or death through starvation. They considered two different situations:

(1) *Cooperative optimum*: Here, all birds scan at the rate that maximizes the fitness for the group. This optimum is thought to be unstable as an individual can "cheat" by feeding more than its flockmates, unless the group is composed of close relatives (Grafen, 1979).

(2) *Selfish optimum*: This is the evolutionarily stable strategy (ESS) (see Maynard Smith & Price, 1973), the scanning rate for which any deviating individual has a lower fitness and so "cheating" does not pay.

Pulliam *et al.* (1982)'s model predicted that selfish birds scan less frequently than cooperative birds. When they compared their model to data, they found the surprising result that the observed scanning rate was closest to the cooperative optimum, even though this should be vulnerable to cheating. Since Pulliam *et al.* (1982), most authors have considered either the group optimum (e.g. Lima, 1987) or the selfish optimum, (e.g. McNamara & Houston, 1992) but not both.

However, in a more general context, many authors have recognized that cooperation can evolve among unrelated, selfish individuals if they repeatedly meet. Axelrod & Hamilton (1981) showed that in the Prisoner's Dilemma Game, the strategy "tit-for-tat" is evolutionarily stable if and only if the interactions between the individuals have a sufficiently large probability of continuing. However, this game only allows the discrete choice of cooperating or defecting, and so cannot be applied to vigilance behaviour. Roberts & Sherratt (1998) consider variable investment and show that cooperation can thrive through a new strategy which they call "raise-the-stakes". This strategy offers a small amount on first meeting and then, if matched, raises its investment. This idea could be applied to vigilance behaviour. Suppose we start off with birds that scan at a low (selfish) level, and then slowly increase this bit by bit only if they find others around them doing the same. This raises the question — why should birds increase their vigilance? There are two possible explanations. Firstly, individuals may wish to preserve their flockmates, so that they are safer from predators in future attacks as a result of the dilution effect, (Lima, 1989). Secondly, if predators are successful, they may be more likely to attack the same flock in the future (Croze, 1970; Sugden & Beyersbergen, 1986; Tinbergen, 1951); therefore it is best for individuals to cooperate to prevent the predation rate from increasing. In this paper we have so far considered only selfish equilibria; however in this section we compare such equilibria with the equivalent cooperative ones. The objective of this section will be to identify the conditions under which the benefits of cooperation are greatest.

5.1. THE GROUP PAYOFF FUNCTION

In the cooperative model we will maximize the net gains from feeding for the group. This is given by

$$f(u,A) = \theta N u\left(1 - \frac{1}{1+\left(A/NZ\right)^m}\right) - yK(1-P)(1-PP_A)^{N-1}.$$

Note that the payoff is always higher for the cooperative birds; if cooperation could be maintained it would be beneficial. Vigilance is higher for the cooperative birds, since each is willing to "do its bit" for the group; however cheats can exploit this by feeding more and the selfish optimum has less vigilance and more feeding. These are general features of the comparison between the two models.

Table 2 shows the optimal strategy and the payoff per bird for a flock of 10 birds for the cooperative and selfish models, when all the default parameters are used. The models predict that selfish birds spend more time feeding and less time scanning than cooperative birds. This is in agreement with the findings of Pulliam *et al.* (1982). Selfish birds also require larger areas,

TABLE 2
Comparison of the group and selfish optimum

	u	A	Payoff per bird
Cooperative	0.797	18.5	7.25
Selfish	0.858	20.8	5.87

possibly due to the increased feeding; and receive a smaller payoff as a result of the increase in predation costs.

Note that the percentage of successful attacks is very different for the two models. For the cooperative model only 1.4% of attacks are successful, whereas for the selfish model 5.5% are successful. The cooperative birds have to feed longer, to obtain the same level of food, and thus would encounter more attacks, but there is still a large difference between the two predation levels.

5.2. COMPARISONS BETWEEN THE COOPERATIVE AND SELFISH MODELS

In general our models predicted that selfish birds scan less frequently, feed in slightly larger areas and receive a smaller payoff. When we varied each of the model parameters in turn we found that both the cooperative and selfish models were affected in almost an identical manner with just a shift in the absolute values. For example, Fig. 9 shows how the two models compare when we vary the attack rate. Note that the shapes of the graphs are the same but that the curve for *u* is slightly higher, the curve for the area per bird is slightly higher and the curve for the payoff much lower in the selfish model. Our model predicts that cooperation has a particular advantage over selfish behaviour when predators are hard to detect, when resources are plentiful, and when communication is good. Thus in these circumstances it may be more likely for cooperation to emerge in practice.

Our model predictions imply that it is very difficult to distinguish between cooperative and selfish behaviour in real populations since both types of population would react to the changing of any (possibly controlled) factors in a similar way. On the other hand, it may help explain why past theoretical work has produced sensible results whether a cooperative or selfish model was assumed, and that the question of which type of behaviour is truly occurring, though of great interest in itself, may not be crucial for predictive purposes.

6. Discussion

The models developed in this paper are a modification of the spatial model of Proctor & Broom (2000). The main difference between the models is in how the difference in the effectiveness of vigilance for large and small areas is incorporated. Proctor & Broom (2000) assumed that the time taken to make an anti-predatory scan increased with the circumference of the group area. This is not always a reasonable assumption, and in this paper we have introduced a more generally realistic effect; that of worsening communication over longer distances. We now compare the two models [note that Proctor & Broom (2000) considered a cooperative model].

Proctor & Broom's model predicted that a flock of ten birds should spend about 80% of the available time feeding, compared to 86% for our model. The predictions for the area are also different, with the optimal area for our model being 18.5 m^2 compared to that of Proctor & Broom (2000) being 24.3 m^2. In general, the cost of a large area is more severe in our model, so

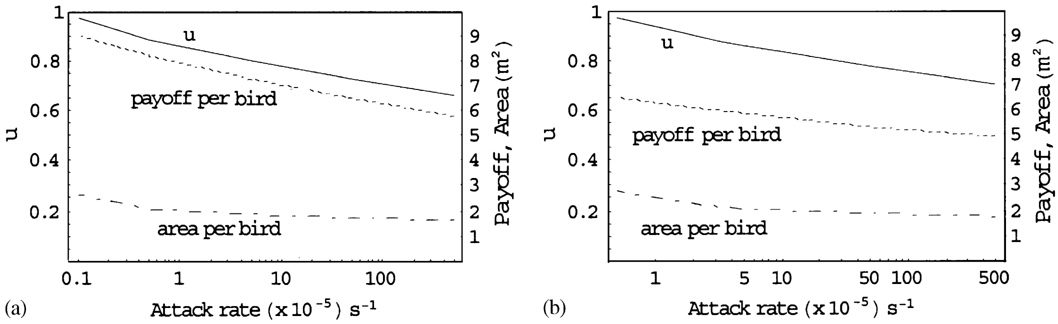

FIG. 9. Comparison of the cooperative and selfish models when the attack rate was varied for a flock of 10 birds. (a) The cooperative model. (b) The selfish model. The value of *u* is indicated by the left-hand scale, the values of the payoff and the area by the right-hand scale.

that areas tend to be smaller. But this also means that the area has more of an effect in our model; for instance the group payoff varies much more with the area than in Proctor & Broom (2000) (see Fig. 3), as does the optimal area for various parameters (e.g. see Fig. 5).

Although our models appear to use the area occupied by a flock as a variable under selection, we realize that it is clearly not the case that flock area per se is under natural selection. Flock area is an outcome of the set of individual decisions about nearest-neighbour distance. However, the choices of nearest-neighbour distance clearly affect the total area of the group. We have used flock area rather than individual neighbour distance as this is much simpler to model.

In our models so far we have only explored how a flock of birds should space themselves in order to maximize their net energy gains by having enough space in which to feed but being close enough to neighbours to permit good communication. It would be interesting to examine how individual variation in optimal nearest-neighbour distance is resolved within a flock and how this would affect the overall spacing of the flock. An important aspect that would need to be considered is the possibility of conflict between individuals with respect to position within the flock. Birds in the centre of the group may experience more interference, whereas those on the edge may be at higher risk of predation. In fact we have modelled this situation and will be submitting our results in a future paper.

In Section 4.3.2, we found that food availability has a large effect on the predictions of the vigilance strategies and optimal area for the group. If food is scarce, then birds need larger areas in which to feed and so nearest-neighbour distances are large making communication more difficult. In this case, our models predict that birds need to be very vigilant and so will be exposed to predators for longer periods. If birds are able to feed close together because food is plentiful, the neighbours make good vigilance mates and so birds can be less vigilant.

In Section 4.3.3, we found that spacing is greatly affected by the predator attack rate for a given flock size, with higher attack rates resulting in birds moving closer together as well as increasing their vigilance. This is in good agreement with observed data. We examined the relationship between attack rate and flock size and considered both a constant attack rate and one that is linear with n. We compared the two relationships in Fig. 8 and found that our model was not very sensitive to changes in the form of this relationship.

In Section 4.3.4, we discussed how the effectiveness of communication between birds may depend on species of bird, shape of the flock and the presence of visual obstructions. Our models predict that increasing the effectiveness of communication allows birds to feed safely in larger areas with decreased vigilance. The communication parameter could also be adjusted to look at the effect of flock shape. As expected, our models predict that birds should move closer together and be more vigilant as the shape of the region becomes more elongated. This is in good agreement with the observations of Bekoff (1995).

We were also interested in what happens when we vary the group size. Many studies have shown that individuals spend less time being vigilant as group size increases and most previous models predict this to be the case. However, there are data that suggest that vigilance does not decrease indefinitely with group size. For instance, in their study of house sparrows, Elgar & Catterall (1981) found that there was no appreciable decrease in scanning rates with flock size for flocks with more than five individuals. In our models the vigilance level and the payoff increases with the number of birds, but both of these quickly flatten out, so that the increases when the number of birds is greater than 30–50, depending upon the model used, become very small. If the predator attack rate increases with flock size, then our model predicts that birds in large groups should feed closer together.

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Appendix

Modelling the Cost of Vigilance as an Energetic Cost

Suppose that a bird suffers death from attacks at rate D, and gains energy at rate E. For simplicity let us assume that its energetic value is K (and this becomes 0 when it dies) and reproduction is proportional to total energy. Then a bird wishes to maximize its energy multiplied by the probability that it is alive.

After time t, this is $(K + Et)e^{-Dt}$.

$$\begin{aligned}(K + Et)e^{-Dt} &\approx K(1 + Et/K)(1 - Dt)\\ &\approx K(1 + Et/K - tD)\\ &= K + t(E - DK).\end{aligned}$$

This is maximized when E-DK is maximized, where E and D depend on vigilance. This is the function that we use in our model, where E corresponds to the left-hand side of eqn (4) and DK corresponds to the right-hand side. This is an example of the idea described in Houston and McNamara (1999, pp. 116–158).