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A spatial model of antipredator vigilance

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Many species of animals have to perform two contradictory tasks: feeding, and avoiding becoming food for others. A large number of theoretical and empirical studies have investigated the trade-off between feeding and antipredator vigilance, especially in birds. An important factor which has been neglected in these studies is that of the area occupied by the flock. If individuals feed close together, competition increases and feeding rates decrease. However, if individuals space themselves widely, then vigilance efficiency goes down and there is an increased predation risk. We develop a vigilance model which allows birds to control the area the flock occupies as well as their vigilance rate. The optimal strategy is found for the birds under a variety of environmental conditions. In particular the effect of each environmental parameter on this optimum is considered in turn. How the model can be adapted for different bird species is also investigated.

Keywords: foraging; predation; spatial model; strategy; vigilance.

1. Introduction

Two major parts of the lives of most animals are foraging for food and attempting to avoid becoming food for other animals. These are often mutually exclusive activities, whereby devoting more effort to one reduces the effort available for the other. For example, a ground-feeding bird must look down to search for food, but look upwards to see approaching predators, such as hawks. Thus when the birds are foraging for food, they divide their time between actually feeding and being vigilant, or *scanning* for predators. A period of vigilance is known as a *scan*.

Many birds form flocks to feed and it has been observed that there is an inverse relationship between individual vigilance and group size. This inverse relationship has been explained by considering two separate effects. Firstly, there is the group vigilance hypothesis whereby members of the flock benefit from the vigilance of other members (Davis, 1975; Lazarus, 1979; Pulliam, 1973). It is assumed that when an individual detects a predator it may pass on this information to its group mates. The warning may be given either as an alarm call or the suddenness of take-off without any preflight movements. Secondly, there is the individual risk hypothesis, whereby members of the flock benefit from the *dilution effect* (Dehn, 1990; Hamilton, 1971). Assuming that a predator only kills at most one victim during an attack, the larger the group, the less likely a particular bird is to be killed. The combination of these two effects increases the benefits of group feeding even

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more (Dehn, 1990; Roberts, 1996). The time saved through reduced vigilance can thus be devoted to foraging (or other activities). There are many other factors which relate to group size and may also affect vigilance behaviour, in which case they may have a confounding effect on the relationship between vigilance and group size; see Barnard (1980), Elgar (1989), and Lima (1987a).

This tendency of birds to forage in groups has generated a significant body of theory (for example, Broom & Ruxton, 1998; Lima, 1987b; McNamara & Houston, 1992; Pulliam *et al.*, 1982). These models find the optimal level of vigilance of birds dependent upon a number of factors, for example, group size and predator attack rate.

The model developed in this paper is concerned with finding the optimal area, as well as the optimal vigilance rate, for a given sized flock. The amount of space required will depend upon a number of factors. Many studies have been carried out on the spacing of wading birds according to type of species, habitat and food density (e.g. Moody *et al.*, 1997; Zwarts *et al.*, 1990).

If we assume that factors affecting area are controlled for (i.e. we look at a particular species, in a particular habitat which extends over a very large area, where the food density remains constant over the region), then we can consider what area of the region the flock should occupy in order to maximize its rate of energy gain. For a given sized flock, the larger the area they occupy, the more food each bird may be able to obtain, although birds may also have to scan more frequently as the size of the region increases. Another disadvantage of increasing the area is that it becomes more difficult for the birds to see all other members of the flock and so they are less likely to be informed of a predator attack. For example, Pöysä (1994) found that near individuals make better vigilance mates.

The shape of the region occupied by a flock is also of interest. This will depend upon 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 as the feeding area will be restricted by the sea, and possibly rocks and pebbles.

In Section 2 the model is described in detail, including a discussion of the pay-off function and each of the model parameters. The predictions of our model are given in Section 3. In Section 3.1 the area occupied is fixed and the best vigilance strategy is found. In Section 3.2 both area and vigilance rate can be chosen by the birds, and the optimal pair is found for our chosen default parameters; how this optimal pair changes when each of the parameter values is altered in turn, and thus the effect of each parameter of the model, is considered in Section 3.3. In Section 3.4 the model is adapted to consider a range of bird species. Section 4 is a discussion of the model predictions, comparing both the data and previous models.

2. The model

2.1 *The pay-off function*

In this paper we develop a simple spatial model in which we assume that there are N birds occupying a region of area A with circumference c. We assume that all birds are scanning at the same rate, regardless of their position within the group. The pay-off function for this model is based on that of Broom & Ruxton (1998). We assume that the birds aim to maximize their rate of energy gain which is: pay-off $= F_g - yKP_{ns}$, where F_g is the rate of food gain of the population, y is the rate at which predators attack (following a Poisson process), K is the cost of a successful attack, and P_{ns} is the probability that the predator is not spotted until an attack commences. It is assumed that an attack is successful if and only if the predator is not spotted prior to the attack. Note that there may also be an energy cost K_1 to the birds even when they escape the predator attack; K can be viewed as the extra cost of a successful attack over and above this fixed cost. Thus there would be an extra term $-yK_1$ added to the pay-off expression. However, this does not vary with the choice of strategy, and so has no effect upon the optimal strategy for our model. Thus it has been ignored.

Evaluation of P_{ns} is as in Pulliam *et al.* (1982),

$$P_{ns} = u^N e^{-(\frac{1}{u}-1)\frac{t_a}{t_s}N},$$

where u is the proportion of time spent feeding; t_a is the time taken for an attack; and t_s is the time taken for a scan.

We assume that the time of a scan depends on the circumference of the region; i.e. $t_s = t_o c$. So

$$P_{ns} = u^N e^{-(\frac{1}{u}-1)\frac{t_a N}{t_o c}}.$$

The rate of energy food gain F_g is given by $F_g = Nu\lambda$, where λ is the rate of food uptake per bird. We assume that λ is an increasing function of A, but that the rate of increase will slow down as A becomes large and it will eventually reach an asymptote. Thus we define the feeding rate, λ, as

$$\lambda = \left(1 - \frac{1}{1 + (\alpha^2 A)^m}\right)\mu, \tag{1}$$

where μ is the maximum feeding rate. The constant α^2 is chosen in this form for mathematical convenience, and m is some positive constant. The value of m determines the relationship between area and the possible rate of food uptake; considering λ plotted against A, a small m gives a curve which approaches the asymptotic value of λ (=μ) slowly, and a high value of m gives a curve which approaches this value quickly. Thus, if m is large, a medium-sized area will allow a bird to feed almost at maximum capacity, and little extra gain will be made by increasing this area.

Suppose that $Z\text{m}^2$ is the area required for one bird to eat at half its maximum feeding rate. Thus, if the total area is NZ, $\lambda = \mu/2$. This gives

$$\left(1 - \frac{1}{1 + (\alpha^2 NZ)^m}\right)\mu = \frac{\mu}{2} \tag{2}$$

$$\Rightarrow \alpha = \frac{1}{\sqrt{NZ}} \quad \text{for all } m.$$

Therefore the feeding rate also depends on N with λ decreasing as N increases for a given area.

Note that, if A is zero, $\lambda = 0$; and, as A approaches infinity, λ tends to μ.

So the pay-off becomes

$$F_g - yKP_{ns} = Nu\left(1 - \frac{1}{1+(A/NZ)^m}\right)\mu - yKu^N e^{-(\frac{1}{u}-1)\frac{t_a N}{t_o c}}. \tag{3}$$

Since we want to maximize the pay-off, this means that we want to minimize the second term in equation (3). Thus we want to make c as small as possible, which is achieved by making the region circular. Since, for a circle, $A = \pi r^2$ and $c = 2\pi r$, then $c = 2\sqrt{\pi A}$. So equation (3) becomes

$$F_g - yKP_{ns} = Nu\left(1 - \frac{1}{1+(A/NZ)^m}\right)\mu - yKu^N e^{-(\frac{1}{u}-1)\frac{\beta N}{\sqrt{A}}}, \tag{4}$$

where

$$\beta = \frac{t_a}{2t_o\sqrt{\pi}}.$$

It is possible to model noncircular regions by having a different relationship between A and c, for example $c = 2\nabla\sqrt{\pi A}$, where $\nabla \geqslant 1$, $\nabla = 1$ indicating a circular region. We will not discuss this generalized case.

2.2 *The model parameters*

We now discuss each of the parameters of the model in turn, and suggest a suitable value for real populations. This is referred to as the default value. In Section 3.3 each of these values is varied to see how this affects the model predictions.

2.2.1 *Group size, N.* The choice for N was rather arbitrary as a flock can be of any size greater than one. We chose the default value to be 10. We are particularly interested in the effects on the model predictions when N is varied.

2.2.2 *Feeding rate, λ and maximum feeding rate μ.* In our model λ is a function of A and so does not have a default value. A default value for the maximum feeding rate, μ, was found by consulting the literature. An empirical study of lapwings gave an estimated feeding rate of 7 J s^{-1} (Barnard & Thompson, 1985). This was the average value over a period from mid-December to mid-January and the standard error was given as ± 1 J s^{-1}. This feeding rate corresponds to λu in our model. Since typical values of u are 0.8–0.9, this corresponds to $\lambda = 8$ J s^{-1}. So a reasonable value for the maximum feeding rate μ is 10 J s^{-1}.

2.2.3 *Attack rate, y.* An estimate of the attack rate was found by consulting the literature. Following Broom & Ruxton (1998) a value of $y = 5 \times 10^{-5}$ attacks per second was used. This corresponds to about 2–3 attacks a day depending on the time of year (i.e. the number of daylight hours).

2.2.4 *Cost of an attack, K.* We define the cost of an attack to be the amount of energy lost if a bird is attacked by the predator and killed. This was assumed to be the amount of energy it would have acquired if it had survived through a season, and we estimated this value as 10^7 J. Thus death is equivalent to having energy level zero.

The parameters μ, y, and K only occur in our model as the ratio μ/yK. In fact μ/yK is dimensionless. We will examine the effect of varying this parameter and this will be interpreted in terms of varying each of the individual parameters.

2.2.5 *Time for an attack,* t_a, *time for a scan,* t_s, *and the parameters* t_o *and* β. Both the values for the time taken for an attack and the time taken for one scan were obtained from the literature (e.g. Lima, 1987b), giving $t_a = 2$ s and $t_s = 1$ s. In our model t_s depends on the circumference of the feeding area, so that $t_s = t_o c$. If we assume that a bird can scan 10 m of the circumference in 1 s then $t_o = 0.1 \, \mathrm{s\,m^{-1}}$. This is probably a reasonable assumption for a medium sized wading bird. We defined the parameter β as $\beta = t_a/2t_o\sqrt{\pi}$. Therefore we obtain a value of about 5 m for β. This parameter is proportional to the length of circumference which a bird can scan in the time taken for an attack. So β may increase either as a result of the time taken for an attack increasing or if a bird can scan more of the circumference in 1 s. It is possible that β varies according to the size of bird; i.e. larger birds would have larger values of β.

2.2.6 *The parameter* Z. A reasonable value of Z for a medium sized wading bird was obtained from the literature (e.g. Barnard & Thompson, 1985) as 1 m^2 (and so using our default value of 10 for N we obtain $\alpha = 0.316$).

2.2.7 *The parameter* m. From equation (1) we have

$$\lambda = \left(1 - \frac{1}{1 + (A/NZ)^m}\right)\mu.$$

Let Z_k be the area per bird which gives a feeding rate $\lambda = k\mu$; i.e. $k = \lambda/\mu$. With this assumption the total area $A = NZ_k$. Therefore,

$$k = 1 - \frac{1}{1 + (Z_k/Z)^m}$$

$$\Rightarrow Z_k = Z\left(\frac{k}{1-k}\right)^{1/m}.$$

With the default values of $Z = 1$, then

$$Z_k = \left(\frac{k}{1-k}\right)^{1/m}. \tag{5}$$

If we plot k against Z_k for different values of m, then all the curves pass through the point (1, 0.5). If $k = 0$, then $Z = 0$; and if $k = 1$, $Z = \infty$ for all m. Due to an inability to obtain an estimate of m from real data, the choice of m is necessarily arbitrary. The chosen default value was 5. Fortunately, the results from the model are reasonably robust to changes in m (see Fig. 2).

Table 1 summarizes all the parameters and shows the chosen default values. The parameters u and A are the proportion of time spent feeding and the feeding area,

TABLE 1

The model parameters

Parameter	Description	Default value
u	Proportion of time feeding	–
A	Area of region occupied by the group	–
B	$\sqrt{A}$	–
N	Number of birds in the group	10
λ	Feeding rate	–
μ	Maximum feeding rate	$10\,\mathrm{J\,s^{-1}}$
K	Cost of an attack	$10^7\,\mathrm{J}$
y	Attack rate	$5 \times 10^{-5}\,\mathrm{s^{-1}}$
t_a	Time taken for an attack	$2\,\mathrm{s}$
t_s	Time taken for a bird to scan for predators	–
t_0	t_s/c	$0.1\,\mathrm{s\,m^{-1}}$
β	$t_a/2t_0\sqrt{\pi}$	$5\,\mathrm{m}$
Z	Area required for one bird to feed at half its capacity	$1\,\mathrm{m^2}$
α	$1/\sqrt{NZ}$	$0.316\,\mathrm{m^{-1}}$
m	A measure of how fast feeding rate increases with area	5

respectively. The parameter B is simply $\sqrt{A}$ and is introduced to make the calculations simpler. These are the parameters that we are trying to optimize and so they do not have default values.

3. Results

3.1 *Finding the best vigilance strategy for a fixed area A*

In Section 1 we described the population as having a free choice of both area and vigilance strategy. However this may not be the case. The area of ground where food is available may be severely restricted due to physical features such as rocks and streams, or simply the fact that food is rich only in a very limited part of the habitat. Thus the birds may have just to fill the whole area and pick the best vigilance strategy for this area. The area occupied A is thus kept constant. The working to find the best u for a given value of A is shown in the Appendix.

The solution for our default parameters as the area A is varied is shown in Fig. 1. It can be seen that the model predicts that for small areas u increases as A increases, and the pay-off is very small. At an area of about $15\,\mathrm{m}^2$, u starts to decrease; i.e. birds become more vigilant but the pay-off continues to increases until the area is about $25\,\mathrm{m}^2$. The pay-off slowly decreases as A increases since costs of increasing A (the longer time needed for scanning) outweigh the benefits (an increase in feeding rate). This indicates that the optimal area will be in the region of 20–$30\,\mathrm{m}^2$, when a pay-off of about $75\,\mathrm{J\,s^{-1}}$ will be obtained. Since the maximum possible pay-off for a flock of 10 birds is $100\,\mathrm{J\,s^{-1}}$, the model predicts that only about 75% of the maximum pay-off will be achieved with the default parameters.

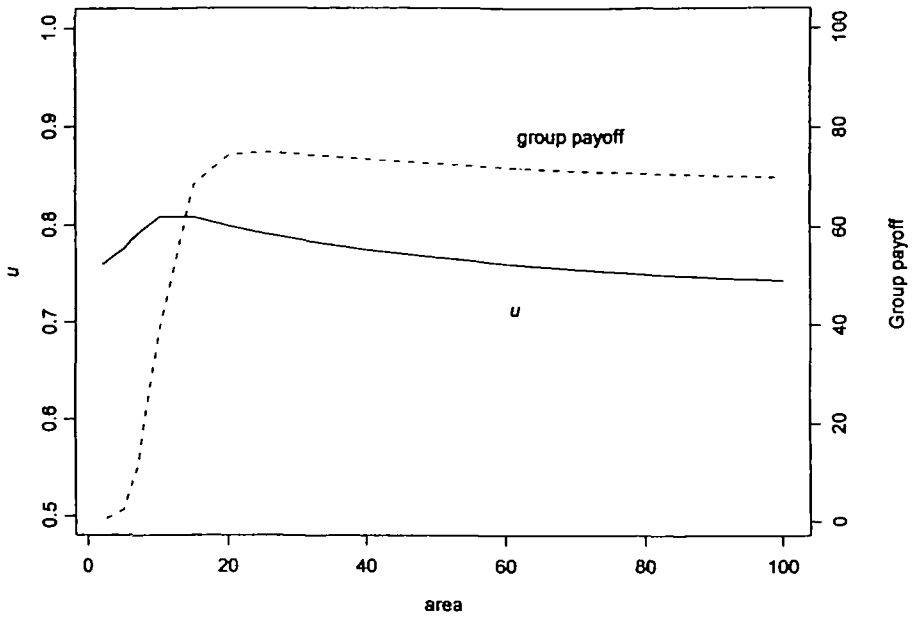

FIG. 1. (—) The optimal value of u and (– · –) the group payoff as a function of area A, using the default parameters.

3.2 *Finding the best combined strategy of area and vigilance rate*

We now return to the case where the area available is large, so that the birds are free to pick the area occupied in conjuction with the vigilance strategy which gives the best return. Thus we want to find the pair (u, A) which maximizes the pay-off.

Note that the total pay-off is always less than $N\mu$, and that the attack rate or the cost of an attack must equal zero in order that a flock of birds obtain the maximum pay-off. In general the group pay-off is given as a percentage of this unattainable maximum.

Details of how the optimal pair and the associated pay-off were found are shown in the Appendix.

Using the default parameters we obtained the optimal pair (0.793, 24.3) with a pay-off of 74.9 for the group. This means that for a group of 10 birds the optimal area is around 24 m^2; they should spend a proportion of time 0.79 feeding and they will obtain about 75% of the maximum pay-off.

Our model predicts that individuals in a flock of size 10 spend about 20% of their time scanning. Since we have assumed that each scan lasts one second, this is equivalent to a scanning rate of about 12 per minute. We can compare these values to actual values from the literature. Powell (1974) found that the proportion of time spent scanning by individuals in a flock of 10 starlings had an average value of 12% (±9%). Barnard (1980) obtained a value of about 20% for a flock of 10 house sparrows feeding in open fields. Elgar & Catterall (1981) also studied house sparrows and obtained an average scanning

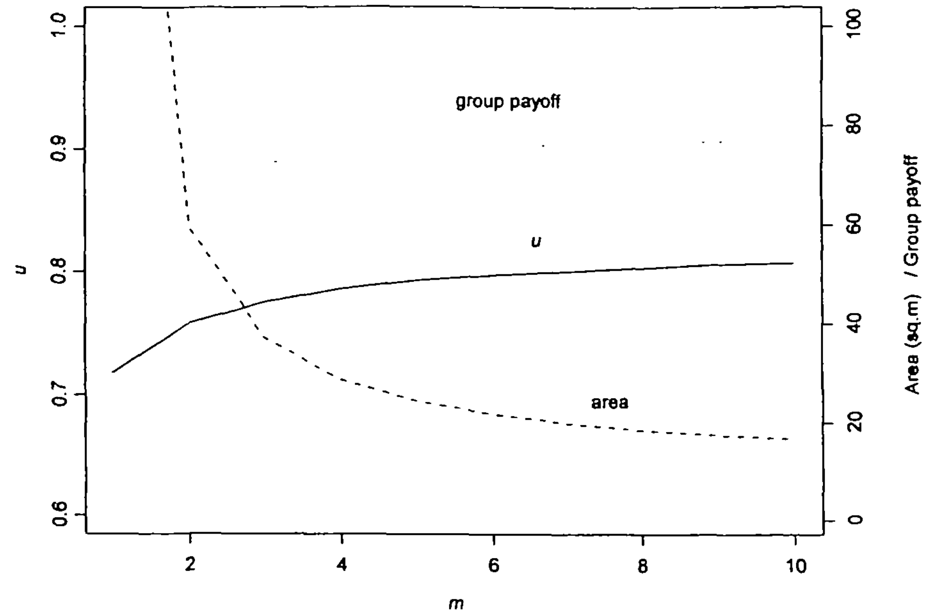

FIG. 2. The optimal values of (—) u, (– · –) the area A, and (···) the group payoff as m is varied (the other parameters take the default values).

rate of about 11 per minute for a flock of 10 birds.

All of these studies agree fairly closely to the value of the scanning rate that we obtained. However, there is data with considerably lower values of scanning rates. Caraco (1979) observed average scanning rates of about 6 scans per minute for a flock of 10 yellow-eyed juncos; Pulliam *et al.* (1982) quote an even lower value of 4.65 scans per minute for the same species. This may be due, for example, to a low attack rate (see Fig. 5 for large μ/yK).

3.3 *Varying the parameter values*

We now investigate how altering the values of each of our parameters changes the results. This is useful for two reasons. Firstly, for some of our parameters (e.g. m) we are not confident of the accuracy of the chosen default values, and for others the values may vary considerably depending upon the conditions (for instance predator density may vary through the year so that y may take a range of values). Secondly, it is of interest to see the contribution of each of the parameters to the optimal play; some may be critical, with small changes leading to large changes in the optimal strategy, whereas the value of others may have little effect.

Each of the parameters N, Z, β, m, and μ/yK are varied in turn to investigate the effects on the model predictions.

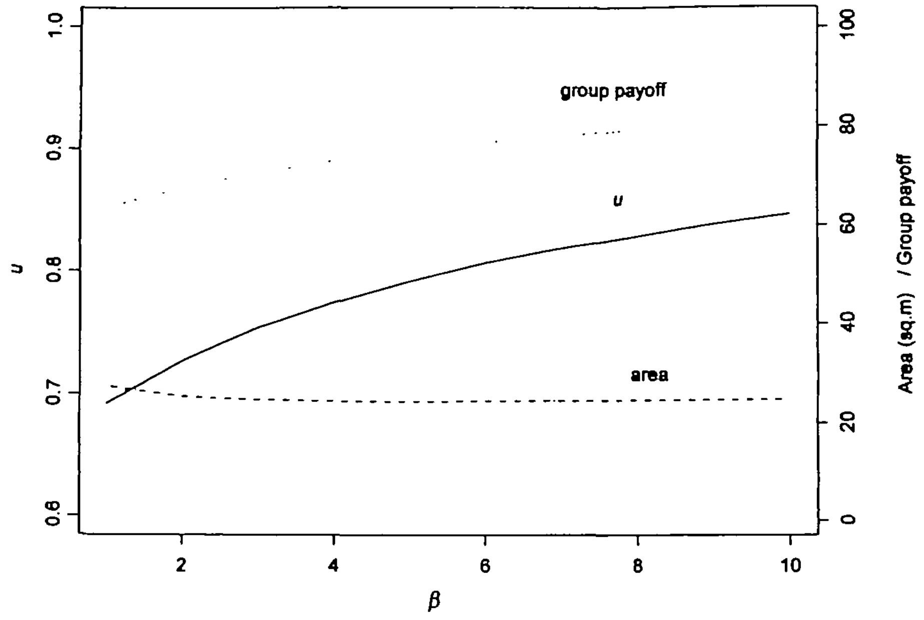

FIG. 3. The optimal values of (—) u, (– · –) the area A, and (· · ·) the group payoff as β is varied (the other parameters take the default values).

3.3.1 *Varying m.* The value of m was varied from 1 to 10 and the results are shown in Fig. 2. It can be seen that as m increases, u increases and A decreases. For $m = 1$–3 the area is very large and for $m > 4$ the values for the area seem more reasonable. There is not much difference in the values of u when $m > 3$. Provided that m is at least equal to 4, the results are fairly robust to changes in m. As we explained in Section 2.2, m had to be chosen in an arbitrary way. It seems from these results that values of m less than 4 are not reasonable, but that any value from 4 to 10 may be.

3.3.2 *Varying β.* The parameter β was varied from 1 to 10 and the results are shown in Fig. 3. It can be seen from Fig. 3 that as β increases then u increases. However, A decreases as β increases from 1 to 5 and then increases again.

The increase in u is what we expected since if either t_a increases or t_0 decreases then birds are safer from attack and so can spend more time feeding. We also expected the area of the group to increase as birds either had more time to scan or could scan more quickly. However, as vigilance rates decrease, the costs of feeding increase *but at a decreasing rate*. Therefore the area decreases initially to compensate. When $\beta = 5$ the costs of increasing u have levelled off and the benefits of increasing the area now outweigh the costs.

We will now interpret the results of varying β in terms of varying the components which make up β.

(1) Increase in attack time. Our model predicts that increasing the time taken for an attack leads to less vigilance. This is in agreement with the predictions of Lima

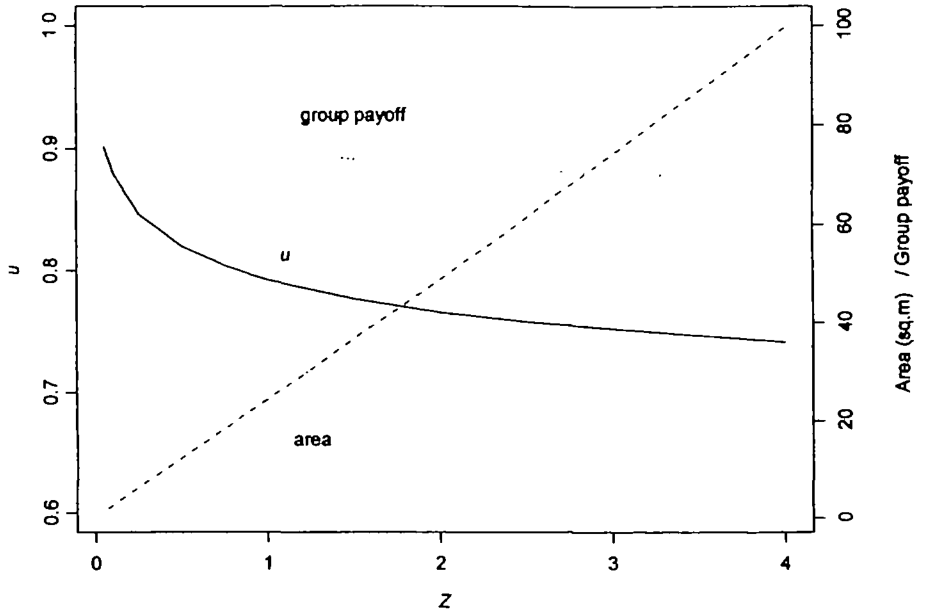

FIG. 4. The optimal values of (—) u, (– · –) the area A, and (· · ·) the group payoff as Z is varied (the other parameters take the default values).

(1987b) and is explained by the fact that lower levels of vigilance will suffice to detect a predator during its long attack time. The area for the group is not greatly affected by changes in the time taken for an attack. We might expect the area to increase as the time taken for an attack increases, due to the increase in the time available for scanning; however, from the model it seems that the best way to take advantage of this is to decrease the vigilance rate rather than increase the area.

(2) Scanning more of the circumference. The amount of circumference that can be scanned in 1 s may depend on the size of the bird. Increasing this amount implies increasing the size of the bird. However, other parameters in the model also depend on the size of bird, e.g. Z. Therefore, we may not be able to interpret increasing β in terms of increasing the size of the bird without altering other parameters in the model.

If we assume that the length of circumference which can be scanned in a given time is independent of bird size, then we can interpret our results by saying that vigilance decreases as more of the circumference can be scanned in a given time but the area is not greatly affected. The area remains roughly constant to compensate for the lowering of vigilance rates.

3.3.3 *Varying Z.* The parameter Z may depend upon the food density; i.e. a lot of food corresponds to small value of Z. The value of Z may also depend on the quality of the

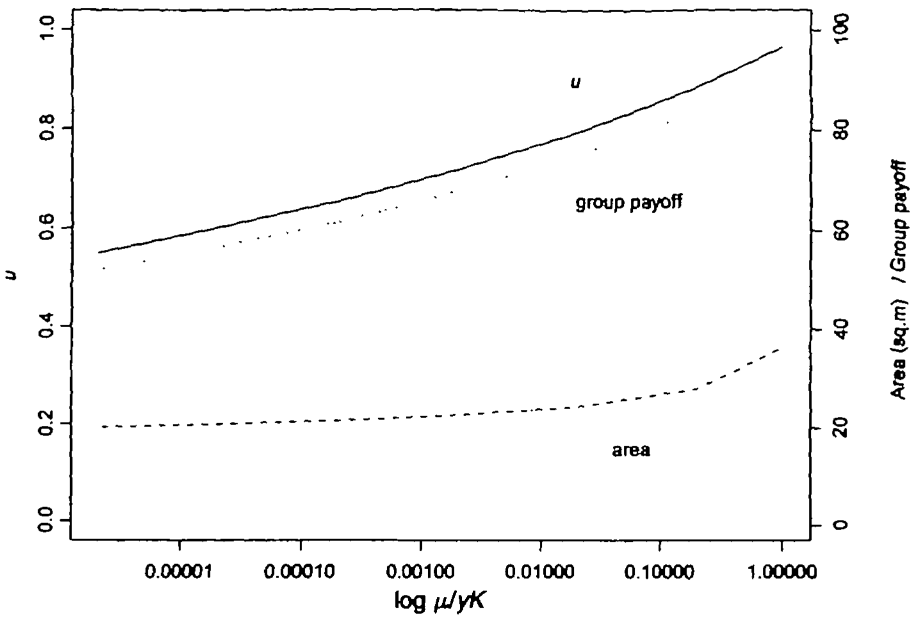

FIG. 5. The optimal values of (—) u, (– · –) the area A, and (· · ·) the group payoff as μ/yK is varied (the other parameters take the default values).

food. Therefore we looked at the effect of varying this parameter with values from 0.05 to 4.0 m^2. The results are shown in Fig. 4.

In general the optimal area increases linearly with Z. To compensate for this the level of vigilance increases, and thus the overall pay-off declines. It can be seen that for small values of Z, the model predicts that birds only need a small area to feed in and that they feed most of the time, obtaining a large pay-off. Such small areas would only be feasible for small birds, such as sparrows, and in this case a small value of β may also be required and so the model predictions for values of Z less than 0.5, say, may not be meaningful. At the other extreme, large values of Z correspond to larger birds and would require a larger value of β.

3.3.4 *Varying* μ/yK. The ratio μ/yK was varied from 2×10^{-6} to 1 and the results are shown in Fig. 5. It can be seen that as μ/yK increase both u and A increase; u increases fairly uniformly, but the increase in A is geometric with only very small increases over the first four orders of magnitude. The increase in μ/yK can be interpreted as either an increase in the maximum feeding rate μ, a decrease in the attack rate y, or a decrease in the cost of a successful attack K.

(1) Increasing the maximum feeding rate μ. As the maximum feeding rate increases then so does the proportion of time feeding and the area per bird. This seems a reasonable result; the birds can gain energy very quickly, so that the length of time they have

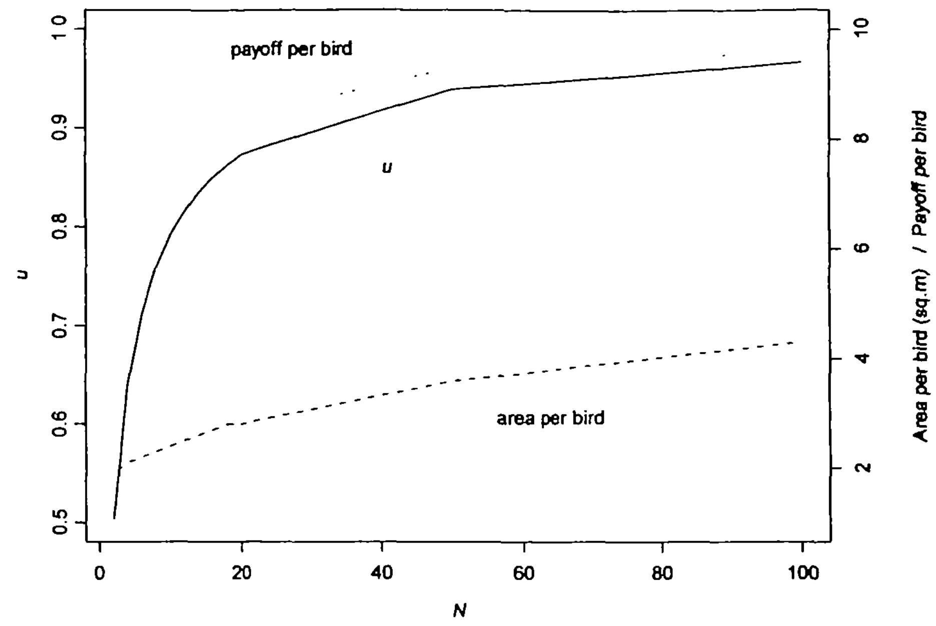

FIG. 6. The optimal values of (—) u, (– · –) the area A, and (· · ·) the payoff per bird as N is varied (the other parameters take the default values).

to spend in the open (and thus being vulnerable) is kept to a minimum. However, the increases are fairly small even if μ increases by a factor of 10. Smaller increases would have little effect on the predicted optimal pair.

(2) Varying the attack rate, y. Our model predicts that a decrease in the attack rate would lead to an increase in the proportion of time spent feeding (i.e. a decrease in vigilance), or conversely an increase in the attack rate would lead to an increase in vigilance. This is a sensible result and agrees with the model predictions of Lima (1987b). However, with all the other default parameters, our model predicts lower vigilance rates than Lima's model for a given attack rate, suggesting that our default values may not be appropriate in this case.

(3) Varying the cost of an attack, K. If the cost of an attack is increased while keeping μ and y constant, then vigilance increases and the area required per bird decreases. This is reasonable, since we would expect birds to be more vigilant if an attack is costly in terms of energy loss. For instance, a strong, healthy bird has more to lose than a starving one, and so should be more vigilant.

3.3.5 *Varying N.* We assume that Z remains fixed as N varies, so that the total area increases linearly as N increases. Figure 6 shows the result of varying N, and it can be seen that the model predicts that u and A increase as N increases. In fact we need to calculate the average area per bird in order to make comparisons, and this shows that the area per bird increases as N increases but with the increase becoming smaller with increasing flock size. Similarly the proportion of time spent feeding increases fairly steadily for small flocks but then increases slowly for flocks larger than 12 birds. Thus the model predicts that vigilance is decreasing with increasing group size, which is what we would expect from previous studies.

Note that it is possible that larger flocks attract a higher level of predation, so as N increases maybe y should also be increased. An increase in y decreases u and A (see Fig. 5), so that there would be a counter-balancing effect. For instance if y is proportional to $\sqrt{N}$, and taking the default value at $N = 10$, the plot looks similar to Fig. 6, but area, pay-off, and feeding rate are slightly lower for large N, and the increase with N in all three is not as marked (when $N = 100$, $u = 0.954$, area per bird is 3.54, and the pay-off is 9.45).

Another, related, possibility is that the attack rate may depend upon the area, with groups occupying larger areas attracting more predators. Supposing that the attack rate is proportional to the circumference of the region, and so to $\sqrt{A}$, then the plot has almost identical shape to that where y is proportional to $\sqrt{N}$. There is some variation depending upon what area gives the default value of $y = 0.000\,05$. In particular, if $y = 0.000\,05$ when $A = 10$, then for $N = 10$ we obtain $u = 0.781$, the area per bird is 2.26, and the pay-off per bird is 7.35. If $y = 0.000\,05$ when $A = 25$, these values are 0.797, 2.28, and 7.50, respectively; and if $y = 0.000\,05$ when $A = 50$, these become 0.809, 2.31, and 7.62, respectively. In general we would expect smaller areas for all of our results, since there is an extra penalty associated with size of area. Comparing the above with our original results from the default parameters indicates that this reduction is not large.

Some empirical studies have shown that birds usually feed closer together in larger flocks. For example, Williamson & Gray (1975) found that the spacing between starlings within flocks was greater in small (spring and summer) flocks than in large winter flocks. Patterson *et al.* (1971) found a similar inverse relationship between flock size and individual spacing in rooks. In both cases, however, this may be explained as a seasonal effect. For instance, in Patterson *et al.* (1971), rooks tended to be in large dense flocks concentrated near the rookeries, mainly feeding on grain. In summer they tended to feed singly or in smaller less dense flocks, scattered over a wide area away from the rookeries, since no grain was available from June to August. Thus the value of Z from our model would be smaller for the winter flocks, allowing the birds to feed at a high rate in a smaller space and so allowing them to feed closer together.

The pay-off per bird increases with increasing flock size and is close to the maximum pay-off of 10 for a flock size of 100. So the model predicts that the bigger the group the better. However, this model assumes that there is unlimited space, which is probably not realistic. Note also that at large flock sizes birds spend very little time being vigilant, which suggests that in this case the dilution effect is more important than the detection effect. Again, very large flocks would probably attract more predators, thus increasing y and so reducing the pay-off, area, and feeding rate.

3.4 *Applying the model for different bird species*

This model was developed for a medium-sized bird, such as a lapwing. However, it is fairly easy to adapt the model for smaller or larger birds. The parameters that are affected by the bird size are: Z, α, K, and μ, and possibly β. Note K and μ only appear in the model in the ratio μ/yK. For a smaller bird, μ would decrease but K would increase by about the same amount. So the ratio remains constant for all sized birds and we do not need to alter the values of either μ or K. It is not clear whether large birds can scan more of the circumference in a given time than small birds. Therefore we will adapt the model for both the case when β is dependent and independent of bird size.

The relationship between metabolic rate and the body size of an animal is well known; a plot of metabolic rates against the logarithm of body mass produces a straight line (Schmidt-Nielsen, 1984). If we assume that metabolic rate is proportional to body surface area then, expressing metabolic rate R as a function of body mass M, in an allometric equation, we obtain $R \propto M^{2/3}$. We shall assume that a bird needs to gain energy proportional to its metabolic rate. Supposing that a bird whose dimensions are x times larger than our lapwing weighs x^3 times as much, its metabolic rate is thus increased by x^2, it needs an area x^2 times as large to feed at half its maximum rate, and so its Z-value is larger by a factor of x^2.

3.4.1 *Case 1: The parameter β varies according to size of bird.* The parameter β may increase with increasing size of bird since a larger bird may be able to scan more of the circumference in a given time. In this section we will compare the size of birds by the ratio of their lengths. We assume that a bird whose dimensions are x times larger can scan x times the circumference in a given time, then we replace β by $x\beta$ in our model. A bird that is larger will also need more food, and following the argument above we replace Z by $x^2 Z$ in our model. Since $\alpha = 1/\sqrt{NZ}$ then we obtain $\alpha = 1/x\sqrt{NZ}$. So equation (A.5) from the Appendix becomes

$$(1-u)\alpha^{2m}\left(\frac{B}{x}\right)^{2m} - \frac{2um}{\beta}\left(\frac{B}{x}\right) + (1-u-2m) = 0. \tag{6}$$

This means that the optimal value of B is now x times larger and so the optimal value of A is x^2 times larger. Therefore we only need to scale the optimal area by a factor x^2, where x is the ratio of the size of the bird compared to a lapwing. Also the optimal value for u is the same for all species of bird. For example a lapwing has length 30 cm and the optimal pair (u, A) for a flock of 10 birds is (0.793, 24.3). An oystercatcher has length 44 cm and so is 22/15 times larger than a lapwing. Therefore the optimal pair (u, A) for a flock of 10 oystercatchers is predicted to be (0.793, 52.3).

Note that, in reality, a bird's mass is not exactly proportional to its length cubed, and that it is more accurate to use birds' real masses (see below). However, these results are approximately correct, and have the advantage of convenience and simplicity.

3.4.2 *Case 2: The parameter β is constant for all species of bird.* Note that some studies have shown that animals spend energy at a rate proportional to $M^{3/4}$ not $M^{2/3}$ (Kleiber, 1932), and Zwarts *et al.* (1990) find the exponent to be 0.723. We shall again assume that the rate at which energy is gained and hence the area needed to supply that energy would vary in the same way. So Z varies with M to some power y, where y may be in the region of 2/3 or 3/4. We have $Z = CM^y$, for some constant C which we can calculate from our default parameters. The mass of a lapwing is about 200 g and this corresponds to $Z = 1$. Therefore $C = 1/200^y$.

TABLE 2

Values of Z for different species of bird when the exponent of the body mass is varied

Species	Mass(g)	Z	
		$y = 2/3$	$y = 3/4$
Blue tit	12	0.153	0.121
Redshank	100	0.630	0.595
Lapwing	200	1.000	1.000
Oystercatcher	500	1.842	1.988

TABLE 3

Optimal strategy when exponent equals 2/3

Species	Z	u	A	Pay-off for the group
Blue tit	0.153	0.865	3.8	83.5
Redshank	0.630	0.811	15.4	77.0
Lapwing	1.000	0.793	24.3	74.9
Oystercatcher	1.842	0.769	45.0	72.2

Therefore

$$Z = \frac{1}{200^y} M^y,$$

and so we can calculate Z for different species of bird if we know their mass. Table 2 shows some approximate masses for four different species of bird and the corresponding values of Z for when $y = 2/3$ and $3/4$.

The optimal strategies when the exponent is 2/3 are shown in Table 3. It can be seen that the model predicts that as the size of a bird increases, then the area required increases; this is what we would expect. It also predicts that the proportion of time spent feeding and hence also the pay-off (as a percentage of the maximum possible pay-off) will decrease as bird size increases.

On average smaller birds do in fact feed more, so this adaptation to the model may be more realistic than when β varies according to bird size. However, birds of different species but of the same size will not necessarily feed for the same proportion of time, as other factors such as type of food eaten and food handling times also need to be considered.

The effect of changing the exponent y is that for birds smaller than lapwings, u increases, A decreases, and the pay-off increases as y increases, but the opposite is true for birds larger than lapwings. It would be possible to find out which value of the exponent is most realistic by comparing the areas used to feed for different species of bird. It would be interesting to find out whether this would give a value close to either 2/3 or 3/4.

4. Discussion

In this paper we have developed a vigilance model which also takes into account the area occupied by a flock of birds. There is a vast literature on the spacing of wading birds feeding along estuaries and also on the vigilance behaviour of flocks of birds. But so far no studies have been carried out which look at the effect of vigilance rates and spacing of flocks of birds simultaneously. Therefore as yet there is no data to test the model which we have developed. It would be difficult to fit the model to data, in order to estimate all our parameters. However, it is easy enough to see how the model's predictions could be tested. For instance if data on vigilance rates, flock area, and flock numbers were obtained simultaneously, then a comparison with our theoretical predictions for the relationship between these from Fig. 6 could be made, since we would expect that the shape of the plots would not depend too heavily on the values of the other parameters.

It has been observed that flocks do vary in how the individual birds space themselves in the flock. If individuals are feeding close together, there is increased competition and feeding rates therefore decrease. On the other hand, if individuals space themselves widely apart, then there will be an increase in the risk of predation. The way in which individuals space themselves obviously affects the total area of the group and so we have looked at the trade-off between small and large group areas. We have assumed that there are no constraints on the area, and that the area will be roughly circular. Thus our model is more appropriate to birds feeding on large areas of grassland than, for example, along the seashore. However it would be a simple matter to adapt the model for elliptical regions.

It can be seen from Fig. 1 that there is an optimal area for the birds to occupy, and this is generally true for a variety of parameter values. The spatial model was developed for a medium-sized wading bird such as a lapwing. It was assumed that a bird of this size would require about 1 m^2 to feed at half its maximum capacity. With this assumption, our model predicted that a flock of 10 birds would spend about 20% of the time being vigilant, and occupy an area of about 25 m^2. This compared well with values obtained from real data.

Obviously many of the parameters in our model can take a range of different values in the real world. Thus the effect of altering the parameter values was investigated, by varying each in turn. In general the solution obtained was fairly robust to alterations in the parameters. As β increases, so that birds are able to spot predators more easily, the area remains roughly the same, but the vigilance rate falls off rapidly, because far less vigilance is required. Increasing Z increases the area a bird requires to feed itself (either the bird is bigger or the food rarer), and thus the required area is almost linear with Z. However when birds occupy a larger area they are more vulnerable, so that the vigilance rate must increase to compensate. The overall pay-off declines because of this. If μ/yK is increased, either the impact of predator attacks diminishes or the value of food increases. There is a steady decrease in vigilance and an increase in overall pay-off as this happens; this agrees with the predictions of Lima (1987b). The area remains roughly constant until μ/yK is very large, then starts to increase as birds become almost totally safe.

We chose a flock size of 10 as the default parameter for our model, but we were particularly interested in what happened when the flock size changed. The model predicted that there was an inverse relationship between time spent scanning and group size, which is in agreement with previous studies and models. The average area per bird also increased slightly with group size. There is safety in numbers both because of the extra eyes to spot predators and the *dilution effect*, so that birds may feel safer to spread out and find more food. Note that in reality, larger groups may mean an increased attack rate, which would counter-balance this effect.

The model was adapted for other species by varying the parameter Z (and possibly also β). When both Z and β were varied, the model predicted that vigilance levels remained the same for all bird species, but that the optimal area increased in proportion to the square of the bird's length. When only Z was varied, the area again increased with the size of bird, but in this case smaller birds spend more time feeding, which is biologically plausible.

The model we have introduced is a first attempt at incorporating spatial factors in the modelling of antipredator vigilance. Our model predicts that the area chosen by a flock of birds is hardly affected at all by some environmental factors, such as the measure of vigilance ability β, but that others such as Z representing food density affect it greatly. Many empirical studies have involved vigilance strategies or the spacing of birds, but none that we know of have included both. We believe that since these two factors are not independent the consideration of both simultaneously in both empirical and theoretical work is of significant value.

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Appendix

A.1 *Finding optimal u for fixed A*

We introduce the parameter $B = \sqrt{A}$ for mathematical convenience.

To find the best value of u we must find the value of u which maximizes the pay-off function. Differentiating the pay-off function with respect to u and setting to zero gives:

$$N\left(1 - \frac{1}{1+(\alpha B)^{2m}}\right)\mu - yKNu^{N-2}\mathrm{e}^{-(\frac{1}{u}-1)\frac{\beta N}{B}}\left(u + \frac{\beta}{B}\right) = 0 \qquad \text{(A1)}$$

$$\Rightarrow \frac{\mu(\alpha B)^{2m}}{1+(\alpha B)^{2m}} = yKu^{N-2}\left(u + \frac{\beta}{B}\right)\mathrm{e}^{-(\frac{1}{u}-1)\frac{\beta N}{B}}$$

$$\Rightarrow \frac{\mu}{yK} = \frac{1+(\alpha B)^{2m}}{(\alpha B)^{2m}}\left(u + \frac{\beta}{B}\right)u^{N-2}\mathrm{e}^{-(\frac{1}{u}-1)\frac{\beta N}{B}}. \qquad \text{(A2)}$$

This equation is easy to solve numerically for u (it can be shown that there is only a single solution).

A.2 *Finding the optimal pair (u, A)*

In order to find the optimal pair (u, A) given values for all the other parameters, we need to find the partial derivatives of equation (4) with respect to u and A. Recall that $B = \sqrt{A}$

and $\alpha = 1/\sqrt{NZ}$. Then we have

$$F_g - yKP_{ns} = Nu\left(1 - \frac{1}{1+(\alpha B)^{2m}}\right)\mu - yKu^N \mathrm{e}^{-(\frac{1}{u}-1)\frac{\beta N}{B}}. \tag{A3}$$

Differentiating with respect to u and setting to zero gives us equation (A.1)
Differentiating the pay-off function with respect to B and setting to zero gives:

$$Nu\frac{\partial\lambda}{\partial B} - yKu^N \mathrm{e}^{-(\frac{1}{u}-1)\frac{\beta N}{B}}\left(\frac{1}{u}-1\right)\frac{\beta N}{B^2} = 0$$

$$\Rightarrow \frac{\partial\lambda}{\partial B} = yKu^{N-2}(1-u)\frac{\beta}{B^2}\mathrm{e}^{-(\frac{1}{u}-1)\frac{\beta N}{B}}$$

$$\Rightarrow \frac{B^2}{\beta(1-u)}\frac{\partial\lambda}{\partial B} = yKu^{N-2}\mathrm{e}^{-\left(\frac{1}{u}-1\right)\frac{\beta N}{B}}.$$

From equation (A.2) we have:

$$yKu^{N-2}\mathrm{e}^{-(\frac{1}{u}-1)\frac{\beta N}{B}} = \frac{\mu(\alpha B)^{2m}}{1+(\alpha B)^{2m}}\frac{1}{(u+\frac{\beta}{B})}.$$

Therefore

$$\frac{B^2}{\beta(1-u)}\frac{\partial\lambda}{\partial B} = \frac{\mu(\alpha B)^{2m}}{1+(\alpha B)^{2m}}\frac{B}{(uB+\beta)}. \tag{A4}$$

Now

$$\frac{\partial\lambda}{\partial B} = \frac{2m\alpha(\alpha B)^{2m-1}}{[1+(\alpha B)^{2m}]^2}\mu,$$

and substituting into equation (A4) gives

$$\frac{B^2 2m\alpha(\alpha B)^{2m-1}\mu}{\beta(1-u)[1+(\alpha B)^{2m}]^2} = \frac{\mu(\alpha B)^{2m}}{1+(\alpha B)^{2m}}\frac{B}{(uB+\beta)}$$

$$\Rightarrow 2mB\alpha(uB+\beta) = \beta(1-u)[1+(\alpha B)^{2m}](\alpha B)$$

$$\Rightarrow 2muB + 2m\beta - \beta(1-u)[1+(\alpha B)^{2m}] = 0$$

$$\Rightarrow \frac{2mu}{\beta}B + 2m - (1-u) - (1-u)\alpha^{2m}B^{2m} = 0$$

$$\Rightarrow (1-u)\alpha^{2m}B^{2m} - \frac{2um}{\beta}B + (1-u-2m) = 0. \tag{A5}$$

The two equations (A.2) and (A.5) in the two unknowns u and A were solved numerically using S-Plus. These results were checked by using an S-Plus routine to maximize equation (4), obtaining the same solutions. This routine also calculated the pay-off.

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