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Modelling responses in vigilance rates to arrivals to and departures from a group of foragers

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Feeding birds must balance food gathering against predation risk. Group foraging is generally considered as a strategy for optimizing this trade-off. Previous modelling studies assumed that group sizes were static and that all group members are informed of an imminent predator attack if one of them detects it. These models implicitly assumed that birds could estimate group size, and adopt a fixed rate of anti-predator vigilance scanning. Recent empirical results suggest that group sizes are generally dynamic rather than static and the group members are often unaware of another's detection of imminent attack. It has also been observed that vigilance rates are not static but change after the arrival or departure of another. Here, we present a model which allows feeding-group size (and individuals' vigilance rates) to vary dynamically, and investigate the implications which this has for the optimum trade-off between foraging and avoiding predation. We find that newly arrived birds should generally be the most vigilant and that vigilance rates should decrease after the arrival of another into the feeding group but increase after a departure. Vigilance rates should increase as the cost of predator attack increases or if the reward rate from foraging decreases. Vigilance should increase if predator attacks are more common but decrease if predators require a longer time undetected to approach the feeding group. In common with many experimental studies, we observe that vigilance rates decrease as the average number of birds feeding together increases. Hence, the main conclusion of previous works (that foraging in groups is an effective strategy for balancing the conflicting pressures of foraging and avoiding predation) is obtained by our model, despite relaxing several previously used assumptions. Finally, we discuss some of the open questions related to group vigilance and how extensions to our modelling framework might be used to address these.

Keywords: co-operation; flocking; foraging; game theory; predation; strategy.

1. Introduction

Most animals (except those at the very top of a food chain) must both forage for their own food and try to avoid becoming food for something else. The requirements of these tasks are often mutually exclusive; for instance, a ground-feeding bird must angle its head down to scan the ground for food but must raise its head in order to be vigilant against predatory

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birds such as hawks. These birds must adopt strategies which allow them to find an effective trade-off between the requirements of foraging and vigilance. Foraging in a group is commonly considered to be one of these strategies (see Roberts, 1996, for a discussion). The assumption is that birds in a group can afford to be less vigilant than solitary individuals, without increasing their vulnerability to predators, because they can take advantage of the vigilance of their group mates. The assumption is that when one individual detects an approaching predator this information is passed to all group members. The time saved through reduced vigilance can be devoted to other activities such as foraging. This possible mechanism has spawned a body of theory (for example, Pulliam *et al.* 1982; Parker & Hammerstein, 1985; Lima, 1987; Packer & Abrams, 1990; McNamara & Houston, 1992).

All the works listed above assume that other group members are informed when one individual detects an approaching predator. This is true for several species of birds where the bird which spots a predator emits an alarm call. However, many other species do not appear to use these calls. Recently, Lima (1995) demonstrated that birds are not always informed of predator sightings by their flock mates. In experiments with starlings, he demonstrated that individuals were unable to differentiate between birds leaving the flock because they feared imminent predator attack and those leaving for other reasons (such as satiation). Lima postulates that birds respond not to unambiguous signals about attack but to the less certain warning provided by an unusually high number of birds leaving the flock within a short period of time. This hypothesis has since been backed up by experimental evidence (Lima & Zollner 1996). Hence, in this paper we will not make the assumption of unambiguous information transfer used by others and will instead assume that individuals use a rule-of-thumb akin to that suggested by Lima. The implication of this for the optimal vigilance rates for individuals will be explored. (Note that it would be easy to adapt our model to use the traditional *alarm-call assumption.*)

Another assumption common to all the previous modelling studies listed above is that the group of birds forms and persists with a stable size. Birds are able to identify this group size and modify their vigilance rates accordingly. This may be true for birds which forage in small stable social or family groups, although even then birds' ability to count is not clearly established (Pepperberg, 1994). However, most groups are not stable but form for a short period of time to exploit a transitory food source. These groups are characterized by dynamic changes in group size due to arrivals and departures. It seems unlikely under these circumstances that birds are able to correctly keep track of group size. However, Roberts (1995) demonstrated that birds are able to detect arrivals and departures, and that they decrease vigilance after an arrival and increase it after a departure. Hence, based on this evidence (and unlike previous works), we will allow the size of the feeding flock to vary dynamically. Furthermore, we will not assume that the birds can determine the group size exactly, although we will assume that they can detect arrivals and departures.

We assume that each individual is characterized by scanning rates under three different circumstances: when they first join the flock, when the last movement was a bird leaving the flock, and when the last movement was a bird arriving. We make no assumptions about the relations between these three rates, but assume that individuals select these rates so as to maximize their long-term fitness (balancing both foraging and predation pressures). An interesting extension would be to examine how a single deviant would behave in such a population.

We have argued that almost all previous models make two assumptions which are not well supported by the available evidence: that group mates are unambiguously informed when one individual detects a predator, and that birds are constantly aware of the group size and modify their vigilance rates accordingly. We present a model which replaces these assumptions with ones which are supported by recent empirical work: birds which do not detect an approaching predator can infer an imminent threat from unusually high levels of departures from the foraging group, and birds do not have a perfect knowledge of group size but modify their vigilance in response to arrivals and departures from the group (which are clearly detectable). We shall use this model to derive predictions about the vigilance levels of individual group members and compare these predictions both with those of conventional models and with empirical observation.

In the next section, we define the model. We then describe the analysis of the model and present some predictions before interpreting these in terms of the underlying individual behaviour. Our aim is to describe how birds should control their scanning rate dynamically during a group-foraging bout, so as to optimize their use of time. Lastly, we discuss how our model predictions fit with previous experimental observations.

2. The model

Consider a group of N birds. The birds occupy a habitat consisting of two areas, a ground-feeding area and cover. Each bird is in one of these two areas at any given point in time (we shall go on to describe the mechanism by which the birds move between the two areas). While in cover the birds are safe from predation but cannot feed. In the feeding area birds are at risk from predation and divide their time between vigilance and feeding, the proportion of time spent feeding being u, which may be different for different birds.

2.1 *Feeding*

While feeding, birds gain energy at rate γ per unit time spent feeding, so that if a bird spends a proportion of time feeding u, it gains food at a rate $u\gamma$.

Each bird which is in cover moves to the feeding area as a Poisson process with rate α, and similarly each bird in the feeding area moves to cover as a Poisson process with rate β. Ideally these rates could depend upon a number of factors; for example, how long the bird had spent feeding, what proportion of the time it had spent in the feeding area, what time of day it is, etc. We assume for simplicity that these rates are constant values (and that feeding is not terminated by factors such as bad weather). In addition, due to predator attacks, all birds in the feeding area simultaneously move to cover as a Poisson process with rate y (see page 390).

In Section 3 we use these processes/parameters to determine the probability distribution of the number of birds in the feeding area, so that we obtain the proportion of all the time potentially available for foraging spent (on average) in any given state. Define $\pi(m)$ as the proportion of time that the number of birds in the feeding area is $m \leqslant N$. Note that it is also important for us to know whether the last event was an arrival or a departure (this affects the birds' strategies), so that we split each state into two, with $\pi(m, a)$ being the proportion of time that there are m birds in the feeding area and that the last event was an arrival, and $\pi(m, d)$ being the proportion of time that there are m birds in the feeding area and that the last event was a departure.

2.2 *Predator attacks*

Predator attacks occur as a Poisson process with rate y. Consider a particular attack. Whilst in the feeding area, a bird that feeds for a proportion of time u, has a probability $g(u)$ of failing to detect the predator during its attack. We assume that the event of a bird detecting the predator is independent of the same event for other birds. If a bird detects the predator the bird leaves to cover. Should more than one bird leave at the same time, the whole group flushes for cover. If no birds or only one bird detects the predator then the predator targets one of the remaining birds at random, and all the other birds go to cover. A bird that is targeted is chased by the predator. We assume that the bird manages to escape to cover but suffers a loss of energy K (equivalently one could assume that the bird is killed, and the *cost of death* in terms of energy is K, in which case for modelling purposes the bird is replaced in the population).

We assume that the length of any attack is small in comparison to the length of time between events (that is, a bird arrives, a bird leaves, or a predator attacks), so that we can treat the whole attack as if it happened at a single point in time, thus the population is in the same state for the whole attack and if more than one bird spots the predator they leave simultaneously causing the whole group to flush for cover. Our assumption means that birds do not flush just because two birds choose to leave at approximately the same time independently of any predators.

Clearly $g(u)$ should be an increasing function of u. We follow the example of Pulliam *et al.* (1982) and define the vigilance behaviour of birds such that they scan for a fixed period t_s in between feeding periods with an exponential distribution whose mean is chosen to make the proportion of feeding time u. Further, a predator requires time t_a to attack and a bird detects the predator if it scans during that time. This yields

$$g(u) = u\mathrm{e}^{-b(1/u-1)}, \qquad b = \frac{t_a}{t_s}.$$

2.3 *Birds' strategies*

In our model, birds do not know the exact number of birds feeding at any one time, but are only aware of other birds arriving and leaving. Thus, a bird is aware of only three different possible states. It is able to choose a different value of u for each of the three states, so that a strategy for a bird when it is in the feeding area consists of a triple (u_1, u_2, u_3), defined as

feed for a proportion of time u_1 if the last event was that the bird arrived,
feed for a proportion of time u_2 if the last event was that another bird arrived, and
feed for a proportion of time u_3 if the last event was that another bird left, respectively.

We examine the case where all birds play the same strategy (that is, all have the same triple (u_1, u_2, u_3)). In Section 3 we evaluate the number of players of each of u_1, u_2, and u_3 in each state, and thus the rate at which the population (or each individual) gains energy and the energetic costs of predator attacks in each state, and thus find the mean pay-off for the population if it plays any given triple (u_1, u_2, u_3). We then find the combination which maximizes this pay-off.

Which triple maximizes the pay-off depends upon the values of various parameters of our model: α, β, y, γ, K, b, and N. In fact it only depends upon six of these values, namely,

$$\alpha, \beta, y, \frac{K}{\gamma}, b, N.$$

3. Mathematical results

We wish to find the pay-off per unit time to the population if it plays strategy (u_1, u_2, u_3); thus we can find the strategy triple which maximizes the pay-off to the population.

3.1 *The time spent in each state*

First, we find the proportion of time $\pi(m)$ that the population spends in state S_m, the state where there are exactly m birds in the feeding area. Later it will be necessary to distinguish between whether the last event was an arrival, represented by state $S_{m,a}$, with proportion $\pi(m, a)$, or whether the last event was a departure, represented by state $S_{m,d}$, with proportion $\pi(m, d)$.

3.1.1 Suppose that the length of time between a given pair of successive predator attacks is T. Each bird acts independently of all others between predator attacks; define $p_T(t)$ as the probability that a given bird is feeding at time t $(0 \leqslant t \leqslant T)$. At the start of the period all birds are in cover (directly after the previous attack), thus $p_T(0) = 0$.

For a single bird, the transition probabilities are as follows, assuming no predator attack. Let F_t be the event that the bird is feeding at time t and $C_t = F_t^C$ be the event that the bird is in cover at time t. Supposing that h is a small time increment

$$\begin{aligned} P(F_{t+h}/F_t) &= 1 - \beta h, \\ P(F_{t+h}/C_t) &= \alpha h \\ &\Rightarrow p_T(t+h) = p_T(t)(1-\beta h) + [1 - p_T(t)]\alpha h \\ &\Rightarrow \frac{\mathrm{d}}{\mathrm{d}t}[p_T(t)] = \alpha - (\alpha+\beta)p_T(t), \end{aligned}$$

with the boundary condition $p_T(0) = 0$.

This yields the solution

$$p_T(t) = \frac{\alpha}{\alpha+\beta}(1 - \mathrm{e}^{-(\alpha+\beta)t}).$$

3.1.2 The probability of a given bird being in the feeding area at time t in our period between predator attacks is $p_T(t)$. Define $P(m, t)$ as the probability that there are exactly m birds feeding at time t; thus

$$P(m,t) = \binom{N}{m}[p_T(t)]^m[1-p_T(t)]^{N-m} = \sum_{r=0}^{N-m}(-1)^r\frac{N!}{m!r!(N-m-r)!}[p_T(t)]^{m+r}.$$

Using the following expansion we get a new expression for $P(m, t)$:

$$(1 - \mathrm{e}^{-(\alpha+\beta)t})^{m+r} = \sum_{l=0}^{m+r}\binom{m+r}{l}(-1)^l\mathrm{e}^{-(\alpha+\beta)lt}$$

$$
\begin{aligned}
\Rightarrow P(m,t) &= \sum_{r=0}^{N-m}\sum_{l=0}^{m+r} \frac{N!(m+r)!}{m!r!(N-m-r)!l!(m+r-l)!}(-1)^{l+r}\left(\frac{\alpha}{\alpha+\beta}\right)^{m+r} \mathrm{e}^{-(\alpha+\beta)lt} \\
&= \sum_{l=1}^{N}\sum_{s=\max(m,l)}^{N} \binom{N}{s}\binom{s}{l}\binom{s}{m}(-1)^{s+m+l}\left(\frac{\alpha}{\alpha+\beta}\right)^{s} \mathrm{e}^{-(\alpha+\beta)lt} \\
&\quad + \sum_{r=0}^{N-m}\binom{N}{m}\binom{N-m}{r}\left(\frac{\alpha}{\alpha+\beta}\right)^{m+r}.
\end{aligned}
$$

3.1.3 We now evaluate the expected amount of time spent in state S_m between times 0 and T. Define this by $L(m,T)$. Then

$$
L(m,T) = \int_0^T P(m,t)\,\mathrm{d}t.
$$

The following integrals are needed to get an explicit value for $L(m,T)$:

$$
\begin{aligned}
\int_0^T \mathrm{e}^{-(\alpha+\beta)lt}\,\mathrm{d}t &= \frac{1-\mathrm{e}^{-(\alpha+\beta)lT}}{(\alpha+\beta)l} \qquad (l>0) \\
&(= T \qquad\qquad\qquad\quad (l=0))
\end{aligned}
$$

$$
\begin{aligned}
\Rightarrow L(m,T) &= \sum_{l=1}^{N}\sum_{s=\max(m,l)}^{N} \binom{N}{s}\binom{s}{l}\binom{s}{m}(-1)^{s+m+l}\left(\frac{\alpha}{\alpha+\beta}\right)^{s} \frac{1-\mathrm{e}^{-(\alpha+\beta)lT}}{(\alpha+\beta)l} \\
&\quad + \binom{N}{m}\left(\frac{\alpha}{\alpha+\beta}\right)^{m}\left(1-\frac{\alpha}{\alpha+\beta}\right)^{N-m} T.
\end{aligned}
$$

3.1.4 We can now find the overall proportion of time spent in S_m, that is, $\pi(m)$. Predator attacks occur as a Poisson process with rate y; therefore the time length x between two attacks follows an exponential distribution with parameter y; the mean value of this time length is thus $1/y$. This implies that $\pi(m)$ is defined as

$$
\pi(m) = \frac{1}{1/y}\int_0^\infty L(m,x)y\mathrm{e}^{-yx}\,\mathrm{d}x.
$$

The following integrals are required to evaluate $\pi(m)$:

$$
\int_0^\infty \frac{1-\mathrm{e}^{-(\alpha+\beta)lx}}{(\alpha+\beta)l} y\mathrm{e}^{-yx}\,\mathrm{d}x = \frac{1}{(\alpha+\beta)l+y}, \qquad \int_0^\infty xy\mathrm{e}^{-yx}\,\mathrm{d}x = \frac{1}{y}
$$

$$
\begin{aligned}
\Rightarrow \pi(m) &= \sum_{l=1}^{N}\sum_{s=max(m,l)}^{N} \binom{N}{s}\binom{s}{l}\binom{s}{m}(-1)^{s+m+l}\left(\frac{\alpha}{\alpha+\beta}\right)^{s} \frac{y}{(\alpha+\beta)l+y} \\
&\quad + \binom{N}{m}\left(\frac{\alpha}{\alpha+\beta}\right)^{m}\left(1-\frac{\alpha}{\alpha+\beta}\right)^{N-m}. \qquad (3.1)
\end{aligned}
$$

3.1.5 We now have an expression for the value of $\pi(m)$ for $0 \leqslant m \leqslant N$. In our model different strategies are played by birds depending upon whether a bird has just arrived, represented by state $S_{m,a}$ which occurs for proportion of time $\pi(m,a)$, or whether a bird has just departed, represented by state $S_{m,d}$, which occurs for proportion of time $\pi(m,d)$.

To be in state $S_{m,a}$, the previous state must have been S_{m-1} (that is, either $S_{m-1,a}$ or $S_{m-1,d}$). The probability that the state of the population goes to $S_{m,a}$ by time $t+h$ given that it was in S_{m-1} at time t is $\alpha(N-m+1)h$, so that the probability that the population moves to state $S_{m,a}$ in period $(t, t+h)$ under steady state conditions is thus

$$\alpha(N-m+1)h\pi(m-1). \tag{3.2}$$

The probability that the state at time $t+h$ is $S_{m,a}$ given that the state at time t is $S_{m,a}$ is $1-[\alpha(N-m)+\beta m+y]h$; thus the probability that the population leaves state $S_{m,a}$ in period $(t, t+h)$ is

$$[\alpha(N-m)+\beta m+y]h\pi(m,a). \tag{3.3}$$

Under the steady state the probability of being in state $S_{m,a}$ does not vary with time, thus expressions (3.2) and (3.3) must be equal. This gives us the value of $\pi(m,a)$ in terms of $\pi(m)$; thus

$$\pi(m,a) = \frac{\alpha(N-m+1)}{\alpha(N-m)+\beta m+y}\pi(m-1). \tag{3.4}$$

From this expression we can also find $\pi(m,d)$, since $\pi(m,d)+\pi(m,a) = \pi(m)$. Alternatively, using similar methods to the above, we can show that

$$\pi(m,d) = \frac{\beta(m+1)}{\alpha(N-m)+\beta m+y}\pi(m+1) \quad (m \geqslant 1). \tag{3.5}$$

3.2 *The pay-off function*

From Section 3.1 all the values of $\pi(m,a)$ and $\pi(m,d)$ have been found. We can now work out the pay-off per unit time for a population playing (u_1, u_2, u_3). If the rate of food gain for the population is labelled as F_g and the probability of the group not spotting the predator (that is, of one or none of the birds spotting the predator) is P_{ns}, then the overall pay-off per unit time is

$$F_g - yKP_{ns}. \tag{3.6}$$

3.2.1 If a bird has just left then all birds play u_3, so that the rate of food gain is $mu_3\gamma$. If a bird has just arrived then that bird plays u_1 and all the others play u_2, so that the rate of food gain is $[u_1+(m-1)u_2]\gamma$. Together this gives

$$F_g = \sum_{m=1}^{N}\pi(m,a)[u_1+(m-1)u_2]\gamma + \sum_{m=1}^{N-1}\pi(m,d)(mu_3)\gamma. \tag{3.7}$$

3.2.2 The probability of the group collectively not spotting the predator is the probability of one or none of the group spotting it. The probability of an individual playing strategy u not spotting the predator is defined as $g(u)$, where $g(u)$ is given by

$$g(u) = ue^{-b(1/u-1)}. \tag{3.8}$$

If a bird has just left then the probability of the group not spotting the predator is

$$g(u_3)^m + mg(u_3)^{m-1}[1 - g(u_3)].$$

If a bird has just arrived, the probability of the group not spotting the predator is

$$g(u_2)^{m-1} + (m-1)g(u_1)g(u_2)^{m-2}[1 - g(u_2)].$$

Together these equations yield

$$\begin{aligned} P_{ns} &= \sum_{m=1}^{N}\{g(u_3)^m + mg(u_3)^{m-1}[1 - g(u_3)]\}\pi(m,d) \\ &\quad + \sum_{m=1}^{N-1}\{g(u_2)^{m-1} + (m-1)g(u_1)g(u_2)^{m-2}[1 - g(u_2)]\}\pi(m,a). \end{aligned} \tag{3.9}$$

Combining equations (3.1), (3.4)–(3.9) we now have an expression for the pay-off per unit time for any strategy (u_1, u_2, u_3). Equation (3.6) gives this pay-off as a function of F_g and P_{ns}. Equation (3.7) gives F_g as a function of $\pi(m,a)$, $\pi(m,d)$, $m = 1, \ldots, N$, and our original parameters. Equation (3.9) gives P_{ns} in terms of the functions $\pi(m,a)$, $\pi(m,d)$, $g(u)$, and the original parameters. Equation (3.8) defines $g(u)$. Equation (3.4) defines $\pi(m,a)$ in terms of $\pi(m-1)$ and the original parameters, and equation (3.5) defines $\pi(m,d)$ in terms of $\pi(m+1)$ and the original parameters. Finally equation (3.1) defines $\pi(m)$ for all $m = 1, \ldots, N$.

3.2.3 The above expressions for the pay-off to the population for each strategy can now be used to find the triple strategy for which this pay-off reaches a maximum. This cannot be done analytically and so it was done numerically for various values of our seven (effectively six) parameters. The results are summarized in Section 4.

4. Results

As has been previously stated, the behaviour of the model is determined by the values of six parameters. In this section, we vary the value of each of these parameters in turn and investigate the effects on the model's predictions. All the other parameters which are not being varied are held constant at the default values given in Table 1.

Figure 1 demonstrates the effect of increasing the cost of predator attack K, or alternatively decreasing the reward rate from foraging γ. As one would expect, as the cost of an attack (relative to the foraging reward rate) increases, birds in the foraging area must spend more time being vigilant and so can dedicate less time to foraging. Notice that birds are more vigilant after the departure of another bird than if the last event was an arrival. This is to be expected because an arrival increases the group size, which benefits all the birds

TABLE 1. *The default parameter values*

Parameter	Default
γ	1
K	1000
b	10
α	1
β	1
N	10
y	0.2

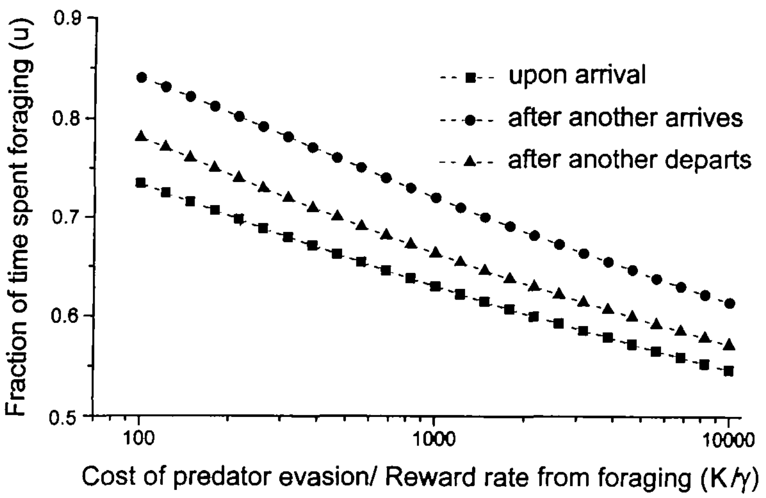

FIG. 1. The value of the optimal population-strategy triple as K varies (the other parameters take the default values).

both because it increases the ability to detect predators and because it reduces the chance of a given individual being singled out by the predator, if an attack is not detected in time. Notice also, that a newly arrived bird is the most vigilant of all. The way the model is implemented, all the other birds in the group must play the same strategy (since for all of them the last event was the arrival of another), the new arrival can play a different strategy. The optimal strategy is for the new arrival to be very vigilant. It is very useful to the population to have one very vigilant individual (this would probably be also true if we assumed that if a predator was spotted it emitted an alarm call), and 'new arrival is very vigilant' is a simple way to achieve this (in our model it is the only way). This means that all other birds can be less vigilant, which provides another reason why birds will be more vigilant after a departure than an arrival, since this extra flexibility does not occur after a departure (all birds play the same strategy after a departure).

Figure 2 demonstrates that individuals need be less vigilant if predators require longer to approach or if the time required for a scan decreases. Again, new arrivals are the most

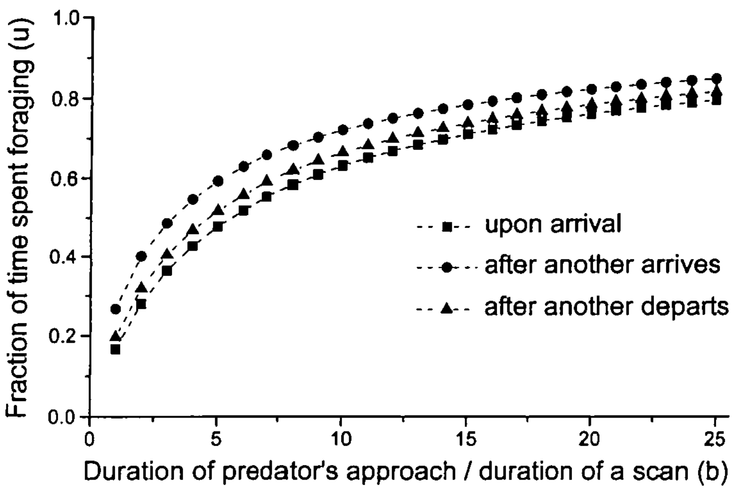

FIG. 2. The value of the optimal population-strategy triple as b varies (the other parameters take the default values).

vigilant, and individuals are the least vigilant after the arrival of another bird. The decrease in vigilance with a fixed increase in approach time, t_a, decreases as t_a increases. This is in accordance with our expectation; one would expect a change in the attack time from 2 seconds to 4 seconds to be more significant than a change from 22 to 24 seconds.

In Fig. 3, increasing the rate of arrivals at the feeding area, α, increases the average size of the feeding group, and so allows individuals to reduce their vigilance rates. When the arrival rates are very low, then the vigilance rates *upon arrival* and *after a departure* are very similar. This is because the number of individuals feeding at any one time will be very low, when an individual first arrives it will often be on its own, similarly after a bird leaves it is likely that any remaining bird will also be alone (after another arrival there are likely to be just two birds). Conversely, when the rate of arrivals, and hence the numbers feeding, is high the vigilance rates *after a departure* and *after an arrival* are very similar. This is because a change of one individual either way makes very little difference in such a large feeding group. The size of the group here is not very variable, in contrast to the case where the total number of birds in the environment (cover and feeding ground) is large (Fig. 4).

As the total number of birds (both in cover and on the feeding ground) increases, so individuals in the feeding area can be less vigilant (see Fig. 4). This occurs because as the total number of birds, N increases, so does the average number of birds in the feeding ground at any given time. Notice that when the total number of birds is very low then birds become more vigilant after a departure than when they first arrive. This is because the probability of foraging alone is higher after a departure than on first arriving, because of the very low number of birds in the system. This is clearly the case for $N = 2$. At the opposite extreme, where the number of individuals in the system is very high, we observe that the birds are more vigilant after an arrival than after a departure. This initially rather counter-intuitive result can be explained as follows. Arrivals are more likely when the number in

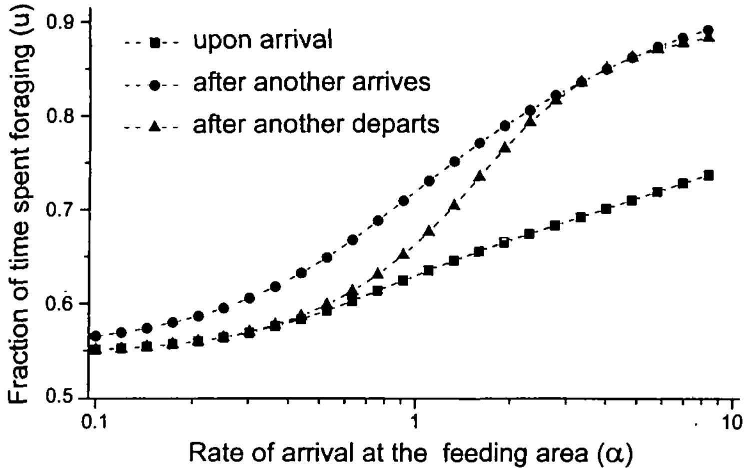

FIG. 3. The value of the optimal population-strategy triple as α varies (the other parameters take the default values).

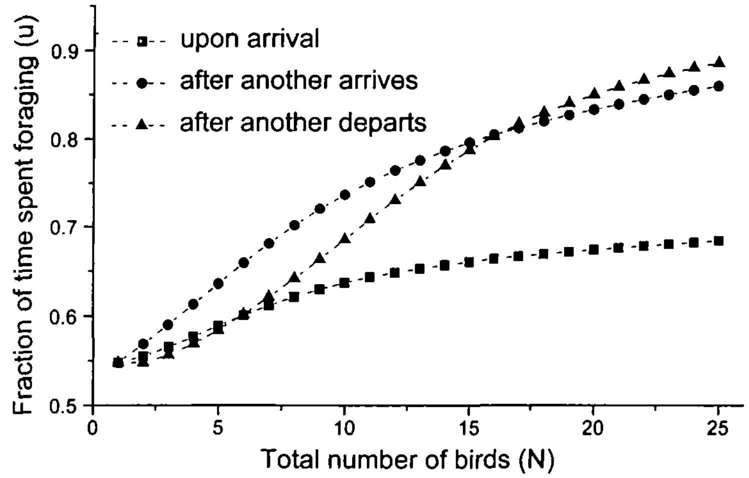

FIG. 4. The value of the optimal population-strategy triple as N varies (the other parameters take the default values).

cover (and hence not in the feeding group) is high; hence arrivals are a 'code' indicating that the current size of the feeding group might be quite low. Similarly, departures signal that the current size of the feeding group is high, and so individual vigilance levels can be reduced (this is only effective when the size of the feeding group is very variable).

Figure 5 demonstrates that vigilance increases as the frequency of departures for non-predatory reasons β increases; this is because the average number of individuals in the feeding area at any one time will decrease with increasing β. As β becomes very high, an

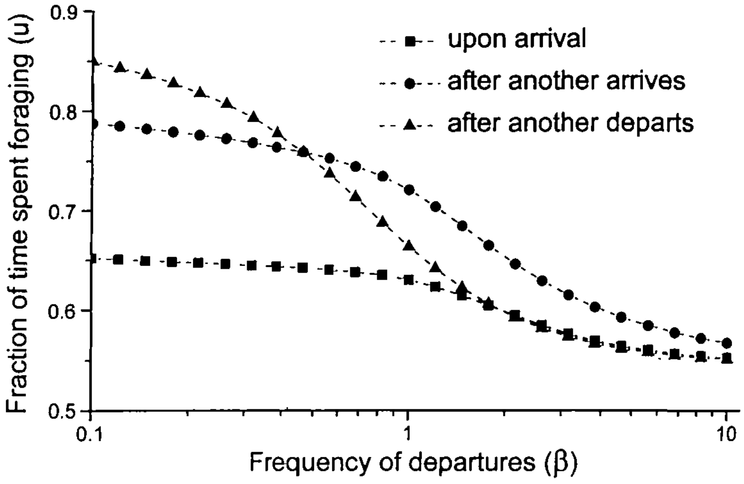

FIG. 5. The value of the optimal population-strategy triple as β varies (the other parameters take the default values).

individual is more vigilant after another leaves even compared to when it first arrived; this is because the departure of another significantly increases the chances that the individual is foraging alone. Conversely, when β is very low, individuals are less vigilant after a departure than after an arrival. The reason is the same as that given for Fig. 4: an arrival is effectively a 'code' indicating that the current size of the feeding group is low. The size of the feeding group is more variable here than in Fig. 3, due to y being relatively large compared to α and β; therefore, the population moves quickly to most birds being in the feeding area (α is larger than β), but returns to zero with a high frequency.

As one would expect, as the frequency of predator attacks increases, individuals are more vigilant (Fig. 6).

5. Discussion

Our observation that birds should generally increase vigilance after the departure of another bird and decrease it after an arrival is in good agreement with the recent field observations of Roberts (1995). Although, interestingly our model predicts that in certain extreme circumstances, birds should adopt the opposite strategy. Similarly, our general prediction that birds would be most vigilant when they first arrive at the feeding ground is in accord with observation of real systems (Lima, 1987). Our third main observation is that vigilance rates should decline as the foraging-group size increases. This is in agreement with many field studies (for example, Burger & Gochfeld, 1992; Lazarus & Symonds, 1992; Cresswell, 1994).

In our model derivation, we have assumed that a bird which spots an approaching predator does not emit an alarm call but simply flies away. We follow Lima (1995) and Ruxton (1996) in assuming that birds which fail to detect the predator will flush for cover if two or more other individuals leave the flock within a short period of time. This seems real-

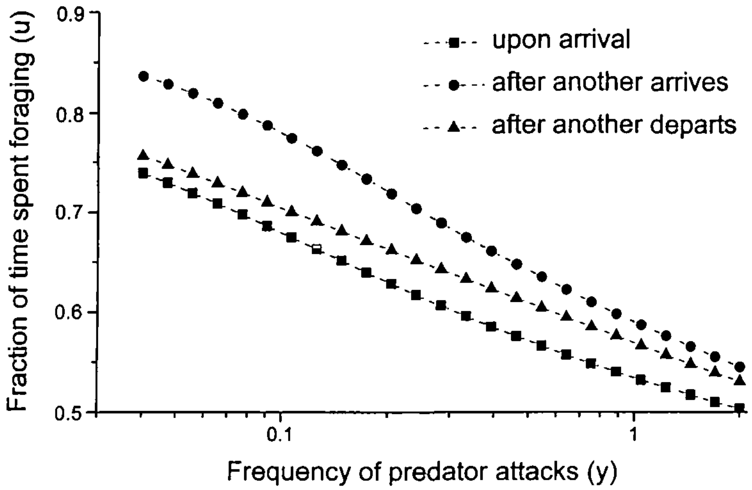

FIG. 6. The value of the optimal population-strategy triple as y varies (the other parameters take the default values).

istic for some species where no alarm calls are given and birds are unable to differentiate between predatory and nonpredatory induced departures, for example, the juncos and starlings of Lima (1996). However, in some species alarm calls or predeparture displays are used (Davis, 1975; Black, 1988; Lamprecht, 1992), and so predator detection by one individual is all the group requires to flush for cover. Our model could easily be adapted to represent such species (indeed the mathematics would be simpler), although we suspect that model predictions will be little changed.

After the departure of another individual, we assume that the remaining birds do not know whether the departure was induced by a predator sighting or not. An effective strategy for the remainder to adopt is to immediately scan for predators, immediately after the departure. Such a tactic has been observed in real populations (Roberts, 1995). One useful extension of the current model would be to allow individuals a greater flexibility of tactics, such as allowing these *checking scans*.

At first sight, our conclusion that birds should become more vigilant (and hence spend less time foraging) when the reward rate from foraging γ is low might seem to be counterintuitive. However, if the fitness-gain rate through foraging is low, it becomes all the more important that birds avoid the considerable fitness loss caused by being singled out in a predatory attack. Birds thus increase their vigilance when the food supply is poor. In practice, birds will have to build up sufficient food reserves before the end of each day in order to see them through the night. This may lead them under some circumstances to adopt a *risk-prone strategy* of reducing vigilance in order to devote enough time to foraging to meet this required reserve. This decision will be based on their current reserves, their estimation of the time remaining until the end of the day, and the expected reward rates from foraging at various intensities. McNamara & Houston (1992) have already demonstrated that such state-dependent vigilance behaviour can have very important effects. Hence, modifying our model to consider the effects of minimum reserve requirements and premature termination of foraging (for example, due to bad weather) should yield a worthwhile and interesting further addition to our understanding of the costs and benefits of group foraging.

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