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Modelling antipredator vigilance and flight response in group foragers when warning signals are ambiguous

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The trade-off between feeding and vigilance in flocks of birds has been extensively studied and modelled. An assumption of many models is that if one bird spots the predator, it gives a signal and the rest of the flock takes flight. However, it has been observed that birds do not always respond to signals and in fact many signals turn out to be false alarms. Since taking flight is both costly in time and energy, it may be advantageous for birds not to respond to all alarm calls. A model is developed to show under what circumstances birds should respond to a signal. The model predicts that under most, but not all, circumstances, birds should respond to multiple detections but not to single detections. The model also predicts that if birds respond to all flights, they will have to compensate for the time lost to feeding and the greater energy requirement of spending more time in flight, by being less vigilant, and they have a lower probability of survival than birds which only respond to multiple detections.

1. Introduction

Animals from a great range of taxa often form groups when foraging. One hypothesized advantage of this is that group membership allows individuals to reduce their personal investment in antipredatory vigilance (and hence increase their foraging rate) without compromizing their risk of predation. One mechanism by which this can be achieved is if the group members that fail to detect an impending attack are informed by those that do. This information transfer could be achieved by vocalizations (so called 'alarm calls') or by the flight of the detector or detectors. There has been considerable theoretical exploration of the consequences of such collective detection on optimal vigilance rates (Pulliam, 1973; Pulliam *et al*., 1982; Lima, 1987; McNamara & Houston, 1992). However, empirical evidence suggests that neither of these information transfer pathways provides the unambiguous signal of impending predator attack that most theory assumes.

Lima (1995) suggested that his experimental birds were unable to differentiate between flights induced by predators and birds taking flight for reasons unrelated to predatory attack. In contrast, Davis (1975) found that pigeons could distinguish between members of the flock leaving in alarm and leaving for some other reason by the absence or presence of pre-flight movements,

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respectively. Pre-flight behaviour has also been observed in pelicans, gannets, boobies and cormorants (van Tets, 1965). Our paper will be discussing a model of flight responses based on studies of wading birds such as redshank which do not have conspicuous pre-flight signals (GDR personal observation), therefore, we will assume that warning signals are ambiguous.

Hilton *et al.* (1999b) report that redshank commonly took flight having apparently misidentified approaching non-threatening birds as predators. This can involve the flight of only a single individual or an entire flock. Similarly, individuals of many species have been recorded emitting alarm calls when no predatory threat can be discerned (Will Cresswell, personal communication). Such false alarms sometimes lead to flocks taking flight, but sometimes do not. Hence, birds in groups do not get the type of unambiguous signal that theory often assumes. Yet, as demonstrated empirically by Hilton *et al.* (1999b), it is clear that birds in a flock can use, perhaps imperfect, information from other flockmates in order to take flight in response to rapidly closing predators. Lima (1995) and Ruxton (1996) suggest that whilst a single departure from a flock presents an ambiguous signal, two or more simultaneous departures are much more likely to have been induced by an approaching predator than any other explanation. Thus, they argue, birds should have an adaptive strategy, whereby their decision as to whether or not to take flight is based on the number of other birds that have just taken off (or, equivalently, alarm called). For simplicity we equate flights and alarm calls, although a more detailed analysis might want to separate the two, since an alarm call is a stronger signal. Although responding to all departures minimizes predation risk, time and energy can be saved if group members only respond to predator-driven departures (Ydenberg & Dill, 1986).

It might be argued that no matter how many false alarms occur, birds should always respond to any signal of a potential attack by taking flight. This 'better safe than sorry' approach, however, would not be practical for many birds. Hilton *et al.* (1999b) report that false alarms are very common in their system, and are certainly much more common than real attacks. Each flight costs the birds both in time and in energy. The latter is particularly important, as flight is a particularly energetically expensive activity. The overwintering redshank are generally very energetically stressed, with starvation being common. Hence, automatic reaction to every potential predatory attack would see birds escape death at the hands of a sparrowhawk only to meet the same fate through being unable to gather sufficient food to meet their needs. Such birds should seek an optimal strategy that maximizes their chance of avoiding death through either of these fates. Here, we present a model that allows us to explore the form of this optimal strategy and how it is affected by ecological parameters. We also assume that the birds can control their individual level of vigilance, and the probabilities of responding to signals from other flockmates. We assume that the birds can adopt different probabilities according to whether a single or multiple flockmates signal.

We seek the strategy which, when adopted by all flock members, minimizes the risk of any individual dying through either predation or starvation. This strategy assumes that individuals cooperate and do not cheat (say by reducing their vigilance rate and taking advantage of the higher rate of others). Lima (1989) shows that non-altruistic cooperation may be stable. This is likely to be true for the behaviour which interests us, namely the response to flights, as opposed to the level of vigilance, since there are clear advantages to behaving as others do (if everyone else leaves, the risk of staying is greatly increased, if everyone else stays it is lessened). Thus we proceed under this assumption.

2. The Model

We consider a population of N birds in a feeding area. We assume that every bird spends a proportion of time feeding u, that each individual within the flock scans randomly and independently of others and that scans take a fixed length of time (Pulliam *et al.*, 1982). Predator attacks, which we will also refer to as 'true attacks', occur at rate α and the probability that any individual in the flock spots the predator is a decreasing function of u, denoted by $f(u)$. The probability that any individual in the flock spots some disturbance, and misidentifies the disturbance as an impending attack, which we will refer to as a 'false attack', is another decreasing function of u, denoted by $g(u)$, where false attacks occur at rate β. Since individuals are trying to spot real predators and $g(u)$ represents misidentification of other movements, it is reasonable to assume that $f(u)$ is always larger than $g(u)$. This means that any given real attack is more likely to be spotted (and reacted to) than any given false attack. It may be that the rate of false alarms increases with the rate of true attacks. This might happen if, as the risk of predation increases, the threshold for accepting a stimulus as representing a predator is lowered. Since false alarms are found to be more common than real attacks (Hilton *et al.*, 1999b), the false attack rate is larger than the real attack rate in our model. Predator attacks typically take about 3 s for the system of a bird of prey attacking a group of birds on the ground (Newton, 1986), and are generally spotted if an individual is vigilant during this time. False alarms consist of both obvious disturbances such as people walking their dogs, and also unseen, by the human observer, disturbing factors (Roberts 1997).

If any member of the flock spots either a true or false attack, then it gives an alarm and takes flight. If no other member of the flock spots the attack, then the individuals in the rest of the flock will respond and take flight with probability Q. However, if more than one bird spots the attack and takes flight, then the rest of the flock respond with probability P. We would expect P to be larger than Q, because multiple detections are more likely to correspond to a "real" attack as opposed to a "false" attack, since $f(u) > g(u)$. If a bird responds to an alarm, it spends time τ_f in flight before it returns to feeding and it incurs a two-fold energy cost: a cost, K due to the energy required to take flight; and also a cost $\tau_f ue$, due to the time lost from feeding, where e is the energy intake per unit time.

The energy gain per individual is eu per unit time, and a day lasts for time T. If birds need minimum energy, M, and the number of alarms responded to is n_1, then a bird starves if

$$Teu - M - n_1(K + \tau_f ue) < 0.$$

This can be rearranged as

$$n_1 > \frac{Teu - M}{\tau_f ue + K} = d.$$

The rate, h, of an individual flying off after an alarm is given by

$$\begin{aligned} h = {} & \alpha[f(u) + \{1 - f(u)\}\{Q(N-1)f(u)(1-f(u))^{N-2} \\ & + P(1-(1-f(u))^{N-1} - (N-1)f(u)(1-f(u))^{N-2})\}] \\ & + \beta[g(u) + \{1 - g(u)\}\{Q(N-1)g(u)(1-g(u))^{N-2} \\ & + P(1-(1-g(u))^{N-1} - (N-1)g(u)(1-g(u))^{N-2})\}]. \end{aligned} \tag{1}$$

This rather long equation will now be explained in detail. The first two lines of equation (1) gives the rate at which an individual will take flight due to real attacks. The attack rate α is multiplied by the probability of taking flight if there is a real attack. This probability is composed of:

1. the probability of taking flight when the individual spots the predator itself, $f(u)$;
2. the probability that it takes flight when it does not spot the predator itself and just one other member of the flock spots it, $\{(1 - f(u)\}$ $\{Q(N-1)f(u)(1-f(u))^{N-2}\}$;
3. the probability that it takes flight when it does not spot the predator itself and more than one other member of the flock spots it, $\{(1 - f(u)\}$ $\{P(1-(1-f(u))^{N-1} - (N-1)f(u)(1-f(u))^{N-2})\}$.

The last two lines of equation (1) give the rate of an individual taking flight if there is a false alarm. These are almost the same as the first two lines, except that we replace α with β, the rate of false alarms, and $f(u)$ with $g(u)$, the probability of spotting a 'false attack'.

If there is more than one bird that decides to remain on the ground when a real attack occurs, then one of these birds is killed by the predator, chosen at random. The risk of death, the product of the attack rate and the probability that a given individual dies during a particular attack, is denoted by k and given by:

$$k = \frac{\alpha}{N}\Bigg[(1 - f(u))^N + N(1 - f(u))^{N-1}f(u) \times (1 - Q^{N-1}) + \binom{N}{2}(1 - f(u))^{N-2}f^2(u)(1 - P^{N-2}) + \cdots + Nf^{N-1}(u)\,(1 - f(u))\,(1 - P)\Bigg]. \qquad (2)$$

The terms in the square brackets give the probability of there being at least one bird remaining on the ground, so that a death occurs. The first term is simply the probability that no one spots the predator, so that everyone stays on the ground; the second term is the probability that no one flies away if only one individual spots the predator, and so on. Equation (2) can be simplified by making use of the Binomial theorem, and after some algebra we obtain

$$k = \frac{\alpha}{N}[1 + P^N(1 - f(u))^N + N(1 - f(u))^{N-1}f(u) \times (P^{N-1} - Q^{N-1}) - \{P(1 - f(u)) + f(u)\}^N]. \qquad (3)$$

After each alarm, a given individual either flies away, stays on the ground but does not get eaten, or stays on the ground and does get eaten. Flying away occurs as a Poisson process with parameter h, and getting eaten occurs as a Poisson process with parameter k. Note that flying away is not quite a Poisson process since after a flight event, another cannot occur for time τ_f, but the approximation is good provided that $h\tau_f \ll 1$. The probability that an individual survives is given by:

$$P(survival) = P[not\ eaten]P[n_1 \leqslant d] = \exp\{-kT\}\sum_{j=0}^{\mathrm{int}d}\frac{(\exp - hT)(hT)^j}{j!} = \exp\{-(k + h)T\}\sum_{j=0}^{\mathrm{int}d}\frac{(hT)^j}{j!}. \qquad (4)$$

We would like to find the values of P, Q and u which will maximize equation (4). First we need to define the functions $f(u)$ and $g(u)$ and then decide on values for all of the model parameters.

2.1. THE PROBABILITY OF SPOTTING ATTACKS

We assume that if a predator attacks, it needs a time t_a s to launch its final uncovered attack. If an individual is vigilant during this time then it spots the predator. As in the previous models (e.g. Pulliam *et al.*, 1982), we define the probability that an individual spots the predator as:

$$f(u) = 1 - u\exp\left(-\frac{t_a}{t_s}\left(\frac{1}{u} - 1\right)\right),$$

where t_s is the time taken for one scan. We will assume that $t_a = 3$ s, as this was the value observed by Newton (1986), and that, as in Proctor & Broom (2000), $t_s = 1$ s. $f(u)$ is a decreasing function in u. We also want the probability that an individual spots a "false" attack, $g(u)$, to decrease with u. Assuming that the false attacks occur instantaneously and are spotted with probability γ by any bird vigilant at the time,

$$g(u) = \gamma(1 - u);\ 0 < \gamma \leqslant 1.$$

We shall mainly consider $\gamma = 1$ in this paper.

2.2. THE MODEL PARAMETERS

To find default values for a bird of prey attacking ground feeding birds, we consulted the literature, (e.g. Lima, 1987; Broom & Ruxton, 1998; Hilton *et al.*, 1999b; Cresswell *et al.*, 2000). The model parameters with their default values are shown in Table 1. We used a flock size of 20 as the median flock size for redshanks was observed to be 23.5 (Hilton *et al.*, 1999b). Obviously, flock size can be very variable and we look at the effects of varying this parameter in Section 4.6. The values for the energy intake and minimum energy requirement were taken from Lima (1987). The minimum energy requirement is crucial in our model and so we also varied this parameter to see how the model predictions are affected (Section 4.2). The attack rate of 2 per day was taken from Broom & Ruxton and the false alarm rate was taken to

TABLE 1
The model parameters

Parameter	Description	Default value
u	Proportion of time feeding	—
P	Probability of taking flight if more than one bird spots the predator	—
Q	Probability of taking flight if only one bird spots the predator	—
N	Number of birds in the group	20
e	Energy intake	0.05 units per sec.
K	Energy needed to take flight	15 units
τ_f	Time spent in flight	360 s
T	Length of day	28800 s
M	Minimum energy requirement	800 units per day
α	Attack rate	2 per day
β	False alarm rate	10 per day
t_a	Time taken for an attack	3 s
t_s	Time taken for one scan	1 s
γ	Proportion of false alarms spotted when $u = 0$	1

be 10 per day, since they are found to be much more common. These values were slightly lower than those observed by Cresswell *et al.* (2000). The time taken for a predator attack is based on observations by Newton (1986) for sparrowhawks, which is the main predator of redshank.

3. Results

The optimal strategy for the default parameters, i.e. the strategy which maximizes the daily survival probability, was found. This gave a probability of survival of 0.99815 per day, when $u = 0.922$, $P = 1$ and $Q = 0$. So the best strategy is for birds to feed for a proportion of time 0.922, and to respond to all alarms when multiple detections occur but to ignore all alarm calls made only by a single individual. The probability of survival that we obtained is close to the value observed in wintering redshanks (Cresswell & Whitfield, 1994). A probability of survival of 0.99815 for 1 day corresponds to a mortality rate of 32.5% for a winter period, (assuming that winter lasts about 210 days (Cresswell & Whitfield, 1994)). This is close to the value of 33.3% for the winter of 1990/91 observed by Cresswell & Whitfield (1994). The maximum probability of survival occurs when only multiple detections are responded to, as in Lima (1994) and Broom & Ruxton (1998), rather than when all alarms are responded to as most other models assume. Note that the probability of survival is 0.996 if the birds respond to all alarms, and in this case they should feed for a proportion of time 0.954. So birds which respond to all alarms should feed more when they are on the ground than those which only respond to multiple detections. The reason for this would be to compensate both for the time lost to feeding and the greater energy requirements of spending more time in flight.

4. Varying the Parameters

We varied some of the parameters in the model while keeping all others at their default value, in order to see how the model predictions were affected. In particular, we would expect the daily energy requirement, M, the predator attack rate, α, and the false alarm rate, β, to affect both how birds should divide their time between feeding and scanning, and how they should respond to alarm calls. We also varied the flock size, N, to see how vigilance varies with group size, and whether or not birds respond less frequently to alarms in larger flocks as might be expected on account of the dilution effect.

4.1. VARIATIONS TO $g(u)$, THE PROBABILITY OF A FALSE ALARM

We briefly consider two possible variations to $g(u)$.

(1) Varying the parameter γ

The parameter γ appears in the function for $g(u)$ and is the probability of detecting a false alarm when $u = 0$, i.e. when a bird is totally vigilant. The results of varying γ are shown in Table 2, and it can be seen that as γ increases, the model predicts that the best value of u increases, and the probability of survival decreases. In each case, the best strategy for P and Q is $P = 1$, $Q = 0$. So our model predicts that as the probability of detecting false alarms increases the birds should be less vigilant. The probability of survival decreases as it becomes more likely that more than one bird actually "spots" a false alarm and so the flock takes flight more often as γ increases. In particular, the larger γ, the larger the $g(u)$ for all u. $g(u)$ is a measure of birds' misidentification and so the larger $g(u)$ is, the worse the birds will perform.

(2) $g(u)$ decreases nonlinearly with u

We also allowed $g(u)$ to decrease nonlinearly with u by letting $g(u) = (1 - u)^2$. This assumes that when birds are totally vigilant ($u = 0$), they will spot every "false attack", but as they start to feed their ability to detect such attacks will greatly decrease. As the birds increase the proportion of time spent feeding, the decrease in detection ability becomes much more gradual. This might be appropriate if birds that are not feeding much ($u < 0.5$) are being particularly wary and so more likely to notice any unusual movements.

The model predicts that the best strategy is for birds to feed for a proportion of time 0.85, and to always respond to multiple detections ($P = 1$), but never to respond to single detections ($Q = 0$). The probability of surviving the day with this strategy is 0.9999958, and so the probability of surviving the winter (assuming that winter lasts about 7 months) is 0.99912. So the winter mortality rate for this model is very low, as the misidentification factor indicated by $g(u)$ is low.

TABLE 2
Results when γ is varied

γ	u	$g(u)$	P	Q	Probability of survival
0.2	0.85	0.030	1	0	0.99999
0.5	0.89	0.055	1	0	0.99981
0.8	0.92	0.064	1	0	0.99893
1.0	0.92	0.080	1	0	0.99815

4.2. VARYING THE DAILY ENERGY REQUIREMENT, M

The total energy requirement for the day is given by the parameter M, and the chosen default value was 800 J per day. This parameter is crucial to the model predictions since the number of times that an individual can respond to an alarm is highly dependent on the amount of food that it needs. The effect of varying M is shown in Table 3. For all values of M considered, apart from $M = 1400$, it is best to always respond to multiple detections and never to respond to single detections. As expected, when energy requirements are low (small M), then birds spend less time feeding and have a high probability of survival. When M is very high then the best strategy is to never respond to alarms and to spend all the time feeding. This seems sensible if a lot of food is required to survive the day, since starvation will definitely kill them, whereas an attack may not, because the predator only takes one individual.

Hilton *et al.* (1999a) noted that birds were less likely to take flight as a result of false alarms, as the daily energy requirements increased. Our model predictions show this indirectly, because as M increases, u increases, which implies that less false alarms are 'spotted' by at least two birds and so responses to false alarms decrease.

4.3. VARYING THE ATTACK RATE, α

We would also expect our model predictions to be affected by a change in the attack rate, α. In

TABLE 3
Results when M is varied

M	u	P	Q	Probability of survival
400	0.85	1	0	0.99999
600	0.89	1	0	0.99980
800	0.92	1	0	0.99813
1000	0.95	1	0	0.98825
1200	0.97	1	0	0.94705
1400	1.00	—	—	0.90484

TABLE 4
Results when α is varied

α	u	P	Q	Probability of survival
0.25	0.92	1	0	0.99985
0.50	0.92	1	0	0.99970
1.00	0.92	1	0	0.99936
2.00	0.92	1	0	0.99813
4.00	0.93	1	0	0.99107
8.00	0.94	1	0	0.94510
16.00	0.97	1	0	0.73804

this section and Section 4.4, we treat α and β as if they are independent, although as we mentioned in the introduction they may not be. See Section 4.4 for a discussion of this. We assumed that there were an average of two attacks per day for our default value. Table 4 shows the results of varying the attack rate. We can see that for all attack rates the best strategy is to respond to only multiple alarms. As the attack rate increases the birds decrease their vigilance and as we would expect, the probability of survival goes down. When the attack rate is very large, the birds have to spend more time feeding to compensate for having to take flight more often and the probability of survival becomes quite low. This situation is unlikely to occur in reality as it would be better for the birds to find somewhere safer to feed.

4.4. VARYING THE RATE OF FALSE ALARMS, β

The default value for the rate of false alarms, β, is 10 per day. Table 5 shows how the model predictions are affected by varying β. When β is very low, then the model predicts that it is best for the birds to respond to all alarms. In this case, the probability of survival is very high since alarms will be quite rare and so birds do not waste much energy from false alarms; also their level of vigilance is fairly high, so that predators will usually be spotted. When the false alarm rate is at least 5, then it is always best to respond to all multiple detections but never to single detections. The model predicts that as the number of false alarms per day increases the flock should spend more time feeding, which will have the effect that less real attacks will actually be spotted, and the probability of survival decreases. We also increased the rate of false alarms and the predator attack rate simultaneously since our treatment of these rates as independent may not be valid. If both rates were very low, then our model predicted that birds should respond to multiple flights only but since flights are rare, they can spend more time being vigilant and the probability of survival approaches unity. On the other hand, if both false and real attack rates are high, then birds should respond to multiple flights only, but flights are very common and as a consequence, vigilance levels have to be lowered and so the probability of survival is low. Thus, the amount of time spent feeding increased and the probability of survival decreased, when both attack rates increased together and when the rates were increased separately. Hilton *et al.* (1999a) found that the rate of false alarm flights in redshank was not based on the actual frequency with which real attacks occurred, but rather depended on the redshanks' ability to detect predators, (e.g. on weather conditions). This suggests that it may be reasonable to consider the false and real attack rates independently.

TABLE 5
Results when β is varied

β	u	P	Q	Probability of survival
2.5	0.88	1	1	0.99999
5.0	0.89	1	0	0.99977
10.0	0.92	1	0	0.99813
20.0	0.95	1	0	0.99064
40.0	0.96	1	0	0.97634

4.5. VARYING THE TIME TAKEN FOR AN ATTACK, t_a

We would expect the time taken for a predator to make an attack, t_a, to affect vigilance levels and also possibly the strategies for taking flight. The parameter t_a appears in the function $f(u)$, which is the probability that an individual spots the predator. The default value was 3 s. Table 6 below shows the result of varying this parameter. As t_a increases from 2, we see that vigilance levels decrease and the probability of survival increases, with the best strategy being to take flight when

TABLE 6
Results when t_a is varied

t_a	u	P	Q	Probability of survival
1	0.94	1	1	0.98701
2	0.92	1	0	0.99515
3	0.92	1	0	0.99813
5	0.93	1	0	0.99954
10	0.95	1	0	0.99998
20	0.96	1	0	0.99999

there are multiple detections. When $t_a = 1$, the birds have little time to spot the predator, so that few birds are likely to spot it; single detections are thus quite likely to be real attacks; and it is best to respond to all alarms. The model also predicts that birds should spend more time feeding; this would be to compensate for more frequent flights.

4.6. VARYING THE FLOCK SIZE, *N*

The results of varying the flock size are shown in Table 7 below. First, we can note that our model predicts that vigilance should decrease with the group size. Second, apart from small flock sizes, it is always best to respond to all multiple detections but never to respond to single detections. When the flock is small, then it is best to always respond to all alarms. This may partly be due to the fact that multiple detections will be much rarer in very small flocks, so that a single detection is more likely to be due to a predator in this case. When flocks sizes are as large as, say, ten birds, then it is more likely that a predator will be spotted by more than one bird and so single detections should be ignored. Lastly, the probability of survival increases with flock size although the increase becomes very small as flock size increases from 40 to 100.

TABLE 7
Results when N is varied

N	u	P	Q	Probability of survival
5	0.86	1	1	0.97650
10	0.86	1	0	0.99367
20	0.92	1	0	0.99813
30	0.945	1	0	0.99903
40	0.959	1	0	0.99941
50	0.966	1	0	0.99952
60	0.972	1	0	0.99957
70	0.976	1	0	0.99961
80	0.979	1	0	0.99964
90	0.982	1	0	0.99966
100	0.983	1	0	0.99968

The fact that our model predicts that only small flocks respond to single detections is consistent with the field data of Roberts (1997). Roberts found that only in flocks smaller than 10, did more than 50% of the flock fly after a single departure. He also found that the larger the flock, the greater the number of individual flights before the whole flock took flight. It would be interesting to modify our model so that it looks at absolute flight numbers instead of just distinguishing between single and multiple detections. This would make the model much more complex but might be worth considering as an idea for future work.

5. Discussion

In this paper, we developed a model to show how birds should respond to alarm calls. We found that our model predicted that birds should always respond to multiple detections but never to single detections for the default parameters and a wide range of parameter values. This agrees with Lima's (1994) hypothesis and empirical work (Cresswell *et al.*, 2000). In particular, the probabilities of survival compared well with Cresswell *et al.* (2000).

By varying some of the model parameters, we found situations in which other strategies were better. If flock size is small, then it is best for birds to respond to all alarms regardless of the number of detectors. This seems plausible as in small flocks it is more likely that there will only be one detector even if there really is a predator. It is also best for birds to respond to all alarms when the time taken for an attack is very short, ($t_a = 1$ s), and when the rate of false alarms is low ($\beta = 2.5$). These predictions make sense because if predators can attack quickly, few birds are likely to spot the predator; and if false alarms are infrequent, then not many flights will take place and so birds can afford to respond to all alarms. So the strategy $P = Q = 1$, i.e. respond to all alarms, was only best in extreme situations, yet it is assumed that birds always use this strategy in many vigilance models (e.g. Pulliam *et al*., 1982; Lima, 1987).

If the amount of energy required to survive the day is very large, ($M = 1400$), then it is best for the birds to spend all their time feeding and so no alarms can be given. This is reasonable as the risk of starvation far outweighs the risk of predation in this case.

Our present model assumes that birds can only detect both false and true alarms when they stop feeding and have a "vigilance" scan. Another possibility is that birds have some ability to perceive predation threats when feeding but this ability is enhanced during non-feeding scans. It may be that false alarms are more likely to occur during feeding, because degraded perception makes differentiation between predators and non-predators more difficult. Such a possibility would make an interesting avenue for future work. Another possibility for future work would be to consider the absolute number of flights rather than distinguishing only between single and multiple flights. This would allow the model's predictions to be more readily compared with the empirical work of Roberts (1997).

We have considered a range of possible response strategies, but only two turned out to be optimal under some circumstances (except in the extreme case when birds are non-vigilant). These are to fly away, if and only if, at least two birds provide a warning, or to fly away if any bird provides a warning. In particular, no intermediate values of P or Q were ever best. This is due to the fact that if any bird remains on the ground, then the predator will make a capture, so that it is optimal for either all birds to fly away or all to stay. All previous papers have assumed one or other of these two models to be true, so it is interesting that these are the only two possibilities that we predict. The evidence of our model is on the side of flying away if at least two birds provide a warning. This is a significant result as most models of vigilance assume that it only needs one individual to see a predator for all to effectively detect it.

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