

## Resource divisibility, predation and group formation

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**Abstract.** A model for foraging groups as a function of physiological state and ecological conditions is developed. The model is motivated by experiments on avian flocks, but applies to other situations as well. The model is based on a dynamic, state variable approach in which a measure of Darwinian fitness is used to relate predation and starvation risks. The experiments concerned the changes of flock sizes when food is added or predators are present, and the observations of Elgar (1986, *Anim. Behav.*, **34**, 169–174) that the divisibility of the resource affects whether birds call for conspecifics upon finding food. The dynamics of flock formation are briefly discussed.

The adaptive significance of living in groups or flocks remains a central question in behavioural ecology. Reviews are found in Krebs & Davies (1984, especially chapter 5), Huntingford (1984) and Barnard & Thompson (1985). In this paper, I concentrate on avian flock formation, but many of the ideas developed here can be applied to other kinds of foraging groups. Thus, throughout the paper, bird and flock are used instead of individual and foraging group. The general answer to the question 'Why feed in flocks?' involves a reduction in individual risk of predation and a reduction in starvation risk through an increase in the rate (or probability) of finding food (Powell 1974; Caraco 1981; Pulliam & Millikan 1982; Ekman 1987a). Both have been studied extensively, although typically as separate phenomena. A recent exception is the work by Grubb & Greenwald (1982), who studied different combinations of predation risk and energy cost on flock sizes. Studies of the general reduction in overall risk of predation are found in Caraco et al. (1980), Stinson (1980), Elgar & Catterall (1981) and Elgar et al. (1984). It is also possible to characterize the process of predator avoidance by mechanistic components such as early detection (Siegfried & Underhill 1975; Lazarus 1979) or vigilance (Elcavage & Caraco 1983; Metcalfe 1984) and defence (Hoogland & Sherman 1976).

Flocking usually increases the chances of finding food (Ekman & Hake 1988). Flocking also provides information (e.g. Giraldeau 1984; Giraldeau & Lefebvre 1987) and leads to social interactions (Davies 1976), which are typically aggressive (e.g. Baker et al. 1981; Ekman 1987b; Metcalfe & Furness

1987). Ancillary advantages of flocking may also occur. For example, birds in flocks may be able to alter their time budgets (Caraco 1979a, b) to enhance overall fitness. The experimental and, to a large extent, theoretical work (see Clark & Mangel 1984, 1986 and references therein) have concentrated on predictions about equilibrium flock size as a function of ecological conditions, rather than a study of the dynamics of flock formation (but see Caraco 1980).

Part of the difficulty in unifying the study of predation and starvation risk (as done by Grubb & Greenwald 1982) is that different 'currencies' are involved, and this makes comparisons of the effects of trade-offs difficult. Recent theoretical work (Mangel & Clark 1986, 1988; McNamara & Houston 1986; Houston et al. 1988), however, has shown how to ameliorate the difficulties by placing starvation risk and predation risk in a framework of Darwinian fitness involving survival and reproduction.

This paper offers a unified theoretical treatment for a series of experimental and field observations by Szekely (personal communication), Grubb (1987) and Elgar (1986, 1987). Szekely studied the response of mixed species flocks to experimental increases in food abundance. When food was added, mean flock size decreased from about 10 birds per flock to about five birds per flock. In general, multi-species flocks broke down upon the addition of food, with fewer species per flock or many birds foraging individually. Szekely also brought a leashed hawk into the foraging area. This led to a rapid increase in flock size. Grubb (1987) reported similar results. Regarding the question of starvation/predation risks,

Grubb concluded that mixed species flocking is caused either by increased foraging efficiency alone or by a combination of increased foraging efficiency and reduced predation risk. In particular, Grubb argued that reduced predation risk alone cannot account for mixed species flocks.

The flocks studied by Szekely and Grubb were formed before food was found. An alternative situation is that birds search individually, but then form flocks after food is found. This could be a result of birds observing each other, and attempting to 'steal' food from the finder (analysed by Clark & Mangel 1984) or a result of the finder calling after finding food. Elgar (1986) experimentally analysed the latter situation and concluded that house sparrows, *Passer domesticus* L., will establish flocks by calling ('chirrup' calls) if resources are divisible. For example, when the food was an eighth of a slice of bread, 14 out of 35 (40%) of the finders called after finding food and this increased to 19 out of 35 (54%) when the resource was half a slice of bread. However, when the eighth of a slice of bread was in crumbs, 27 out of 35 (77%) of finders called other birds. Calling establishes a flock after the resource is located; presumably the reason for calling to establish the flock involves a reduction of the risk of predation. In the follow-up study, Elgar (1987) concluded that 'food intake rate alone is not an adequate measure of the costs and benefits of foraging in groups'. All of these experiments suggest that a full theory must deal with more than food intake rate or predation risk individually; the theory must provide a unified description of the benefits and costs of flocking.

Here, I present such a theory. It allows one to predict how added food, increased predation, colder days, the divisibility of food or any combination of these factors will affect flock size. The theory provides an explanation for changes in group size, as in the experiments of Szekely or Grubb, and for the formation of flocks, as in the experiments of Elgar. I first present the basic model. It is an extension, to include predation, of the model developed in chapter 3 of Mangel & Clark (1988) for social foraging by lions. I consider both divisible resources (which can be shared equally by the flock) and indivisible resources (in which only one flock member obtains the benefit of the food). Next, I consider the situation in which groups are formed before location of resources (modelling the experiments of Szekely and Grubb). I then consider the situation in which resources are

located before groups are formed (modelling the experiments of Elgar); both optimal foraging and dynamic game approaches are discussed.

Caraco (1987) presents work that is similar in spirit, since he considers the divisibility of resources, but concentrates on the effects of social structure (dominance hierarchies) on flocking. Newman & Caraco (1989) also model Elgar's experiments, using two-person game theory. The work presented here differs from theirs in that (1) decisions depend upon the state of the bird and (2) there are  $n$ , rather than two, players involved in the decisions. Thus, the work presented here and that of Newman & Caraco (1989) complement each other.

### BASIC MODEL

Assume that a single state variable  $X(t)$ , 'reserves', describes the physiological state of the bird of interest, called the distinguished bird. For example,  $X(t)$  might represent fat reserves or body weight at the start of day  $t$  in winter. (Nearly all of the experiments of interest take place in winter, so that breeding can be ignored. This means that fitness is the same as viability.) The state variable is constrained by  $x_c \leq X(t) \leq x_{cap}$  where  $x_c$  denotes a critical or starvation level (the bird is dead if reserves fall below this level) and  $x_{cap}$  denotes a maximal capacity for reserves. The theory described below is easily modified for more than one state variable or for situations in which there is no limit to reserves.

The size of the foraging group is denoted by  $n$ . Time is measured discretely (e.g. 5-min intervals or 1-h intervals, as appropriate) and  $\lambda(n)$  denotes the probability that the group of size  $n$  encounters resources in a single period. An explicit model for the encounter probability is

$$\lambda(n) = 1 - \exp(-\varepsilon n) \quad (1)$$

In this equation,  $\varepsilon$  is an operational parameter (Mangel 1985), in the sense that it can be measured in terms of operational characteristics. That is

$$\varepsilon = (\text{area covered per unit time}) \times (\text{food density}) \quad (2)$$

In this equation, the area covered per unit time is determined by multiplying the detection width of the bird by its searching speed. The units of  $\varepsilon$  are thus 1/time; 1 unit of time is explicitly assumed in equation (1).

The dynamics of  $X(t)$  depend upon metabolic costs and the nature of the resources. In each

period, there are fixed and state-dependent decrements (costs) to the state variable. In particular, if  $X(t) = x$ , then if no food is found, the state variable decreases to  $ax - a_0$ . Here  $a \leq 1$  measures reserve-dependent foraging cost and  $a_0$  represents a fixed cost. The fixed cost  $a_0$  represents energy expended for basic physiological function. The variable cost  $ax$  assumes that further energy expenditure increases linearly with reserves.

If resources are divisible, then when food is found each of the  $n$  birds in the flock obtains  $1/n$  of the resource (the effects of changes in this assumption are discussed in the next section and in the final section). Letting  $Y$  denote the value of the resource measured in the same units as  $X(t)$  gives the dynamics

$$X(t+1) = \begin{cases} aX(t) - a_0 & \text{with probability } 1 - \lambda(n) \\ aX(t) - a_0 + Y/n & \text{with probability } \lambda(n) \end{cases} \quad (3)$$

In equation (3), and all subsequent ones, it is understood that if the right-hand side is less than  $x_c$ , then it is set equal to  $x_c$ , or if the right-hand side is greater than  $x_{cap}$ , then it is set equal to  $x_{cap}$ . In computations, it is helpful to use the 'chop function' defined by Mangel & Clark (1988) and described below.

If indivisible resources are found, then only one of the  $n$  birds in the flock obtains the food when it is encountered. Let  $p_g(n)$  denote the probability that the distinguished bird obtains the food. There are now two ways in which the bird ends up with no food in a period: either the flock does not find food at all (with probability  $1 - \lambda(n)$ ) or the flock finds food, but the bird does not get the food (with probability  $\lambda(n)(1 - p_g(n))$ ). The dynamics of  $X(t)$  are now

$$X(t+1) = \begin{cases} aX(t) - a_0 & \text{with probability } 1 - \lambda(n)p_g(n) \\ aX(t) - a_0 + Y & \text{with probability } \lambda(n)p_g(n) \end{cases} \quad (4)$$

The mean rate of food intake for divisible resources is  $r(n) = \lambda(n)Y/n$  and for indivisible resources is  $r(n) = \lambda(n)p_g(n)Y$ . Formally at least, we can identify the means as equivalent if  $p_g(n) = 1/n$ , but this may not be appropriate since it gives each bird an equal opportunity of obtaining the food once it is found. There may be an advantage to the

finder; below I show one way to model this finder's advantage. Depending upon the form of  $\lambda(n)$  and  $p_g(n)$ , the  $r(n)$  may be a decreasing function of  $n$  or a humped function of  $n$  (see Clark & Mangel 1986). If  $r(n)$  decreases for all values of  $n$ , then, based solely on feeding considerations, the bird should forage alone and other factors (variance reduction, predation risk) become extremely important as determinants of flock size.

The probability of a successful attack by a predator in a single period is denoted by  $\beta(n)$  and defined by

$$\beta(n) = \text{Prob}\{\text{predator successfully attacks a flock of size } n \text{ in a single period}\} \quad (5)$$

Assuming that each bird is equally susceptible to predation, the probability that the distinguished bird in a flock of size  $n$  is killed by a predator during a single period is  $\beta(n)/n$ .

Consider a foraging interval of length  $T$  and let  $\varphi(x)$  determine the fitness of the bird at period  $T$ . The choice of  $\varphi(x)$  depends upon the interval that is modelled. For example, when considering a small bird in winter, the natural interval may be 1 day, in which case  $\varphi(x)$  is the probability that the bird survives overnight when its terminal reserves are  $x$ . Alternatively, one might consider the entire winter period, in which each increment in time corresponds to 1 day. Then  $\varphi(x)$  would represent the expected reproduction for a bird with terminal reserves equal to  $x$ . In either case, introduce a fitness function  $F(x, t, T)$  measuring the maximal expected value of  $\varphi(X(T))$ , given the current time and reserve level

$$F(x, t, T) = \max E\{\varphi(X(T)) | X(t) = x\} \quad (6)$$

In this equation,  $\max$  denotes the maximum taken over all behavioural decisions (size of flock to join or whether to call or not) between  $t$  and  $T$ , and  $E$  followed by  $\{ \}$  denotes the expectation taken over stochastic events (finding food, predation) of the quantity within the brackets. From the definition of the terminal fitness function we have

$$F(x, T, T) = \varphi(x) \quad (7)$$

and fitness for preceding values of  $t$  are determined by solving the equation that  $F(x, t, T)$  satisfies. In deriving the equation for  $F(x, t, T)$ , it is helpful to use the chop function introduced by Mangel & Clark (1988). This is

$$\text{chop}[x; a, b] = \begin{cases} a & \text{if } x < a \\ x & \text{if } a \leq x \leq b \\ b & \text{if } x > b \end{cases} \quad (8)$$

This function 'chops' the value of  $x$  in the sense that, regardless of the input value, the output of the function is always between  $a$  and  $b$ . As will be seen below, this function allows us to simplify the equations for fitness.

### FLOCKING BEFORE FORAGING STARTS

When groups are formed before foraging occurs, the designated bird must decide the size of the flock to join at the start of each period. (This raises the question about the dynamics and stability of flock formation; see Discussion or Caraco 1980.)

For divisible resources, the equation that  $F(x, t, T)$  satisfies is

$$F(x, t, T) = \max_n \begin{cases} \text{No predation} & \text{Food is found by flock} \\ (1 - \beta(n)/n) \{ \lambda(n) F(x', t+1, T) + (1 - \lambda(n)) F(x'', t+1, T) \} \\ \text{Food is not found by the flock} \end{cases} \quad (9)$$

In this equation,  $x' = \text{chop}[ax - a_0 + Y/n; x_c, x_{\text{cap}}]$  and  $x'' = \text{chop}[ax - a_0; x_c, x_{\text{cap}}]$ , where chop is defined by equation (8). Cues to interpreting the terms in equation (9) are given above the various terms. To have any fitness in period  $t+1$ , given that its current reserves are  $x$ , the bird must first avoid predation during period  $t$ . This occurs with probability  $1 - \beta(n)/n$ . Then, if the flock finds food, the state variable is incremented by an equal share of the food  $Y/n$ ; this is the second term on the right-hand side of equation (9). Finally, if the flock does not find food, then the state variable is decremented.

For the case of indivisible resources, the equation for  $F(x, t, T)$  is

$$F(x, t, T) = \max_n \begin{cases} \text{No predation} & \text{Food is found by flock, individual gets it} \\ (1 - \beta(n)/n) \{ p_g(n) F(x', t+1, T) + (1 - p_g(n)) F(x'', t+1, T) \} \\ \text{Food is found by flock, individual does not get it} \\ \text{Food is not found by flock} \\ + (1 - \lambda(n)) F(x'', t+1, T) \end{cases} \quad (10)$$

In this equation  $x' = \text{chop}[ax - a_0 + Y; x_c, x_{\text{cap}}]$  and  $x''$  is defined as in equation (9). Note that the terms involving  $\lambda(n)(1 - p_g(n))$  and  $1 - \lambda(n)$  could be combined into  $1 - \lambda(n)p_g(n)$  as described above.

Equations (9, 10) are solved subject to the final condition given by equation (7), for  $t$  ranging from  $T-1$  to  $t=1$ . As these equations are solved, we obtain optimal decisions as well as the fitness function in each period  $t$ . The optimal decisions give the size of a flock of which the distinguished bird should be a member. This is analogous to the optimal group size computed by Clark (1987) for lion foraging groups. For numerical computations, the terminal function was chosen to be  $\phi(x) = x/(x+0.1)$ . Since this function is bounded by 0 and 1, it can be viewed either as a terminal viability or a scaled reproduction when  $X(T) = x$ . In addition, the following parameters were used for computations:  $x_c = 2$ ,  $x_{\text{cap}} = 10$ ,  $\varepsilon = 0.1$ ,  $Y = 4$ ,  $T = 20$ ,  $\beta(n) = 0.005$ ,  $p_g(n) = 1/n$ ,  $a_0 = 0.5$  and  $a = 0.95$ . These choices of  $a$  mean that a bird at capacity would use 1.5 units, about 15%, of its reserves in a period. Table I shows basic results.

From this table, we draw the following conclusions, which are summarized as general predictions in the final section.

(1) Flock size increases as  $t$  approaches  $T$ . This is an effect of the predation/starvation trade-off. As  $t$  gets closer to  $T$ , the chance of starvation decreases (fitness being assessed at time  $T$ ), so the predation risk becomes relatively more important. This is reflected in larger flocks for indivisible resources at  $t = T-1$  but smaller flocks for indivisible resources when  $t = 1$ .

(2) Except for the values of  $t$  that are close to  $T$ , the results show that flocks foraging on divisible resources will be larger than those foraging on indivisible resources (cf. Recer & Caraco 1989). These results can be interpreted in terms of risk spreading (there are two risks that must be considered) or as mean-variance trade-offs.

(3) The fitness values provide a simple measure of selection pressures for the flock foraging. In particular, the selection pressure for flock foraging on divisible resources is considerably higher than the selection pressure for flock foraging on indivisible resources. (A measure of the selection pressure is the ratio of fitness functions; that is  $0.61/0.92 = 0.663$  and  $0.61/0.64 = 0.95$ .) A more complex measure of selection pressure weights  $F(x, 1, T)$  by the probability that  $X(1) = x$  and gives similar results. In particular, the results show that a bird that always foraged alone would not survive for very long. This does not mean, however, that solitary foraging will never occur. Birds will forage alone when their reserves are sufficiently low.

**Table I.** Optimal group sizes when flocks are formed before foraging occurs

$x$	Optimal flock size for:	
	Divisible resources	Indivisible resources
At $t = 1$		
3	3 (fitness = 0.21)	1 (fitness = 0.12) (0.12)*
4	3	1
5	3	1
6	3 (0.66)	1 (0.40) (0.39)*
7	5	2
8	6	2
9	6	3
10	6 (0.92)	5 (0.64) (0.61)*
At $t = T - 1$		
3	10 (fitness = 0.85)	2 (fitness = 0.66) (0.60)*
4	10	12
5	10	15
6	13 (0.98)	15 (0.98) (0.977)*
7	15	15
8	15	15
9	15	15
10	15 (0.99)	15 (0.99) (0.98)*

\*These are the fitnesses of a bird that always forages alone.

**Table II.** Response of optimal flock size to changes in parameters

$x$	Base case		$Y \times 2$		$\varepsilon \times 2$		$\beta \times 4$		$as \times 2^*$	
	D†	I†	D	I	D	I	D	I	D	I
3	3	1	6	1	4	1	3	1	1	1
7	5	2	11	2	7	1	7	3	1	1
10	6	5	12	6	10	5	7	12	3	2

\*Recall that:  $Y$  = size of food found,  $\varepsilon$  = search parameter in finding food;  $\beta$  = predation rate;  $as$  are metabolic costs.

†D: divisible resources; I: indivisible resources.

When  $T = 20$ , by  $t = 1$  the decisions of the birds about flock size depend only upon the value of the reserves and not explicitly on time. Although the decisions are stationary, there is no stationary value to the fitness function, which has the property that as  $T$  increases,  $F(x, 1, T)$  gets smaller for fixed  $x$ .

Computer experiments (Mangel & Clark 1988) can be used to study the effects of changing parameters on optimal flock sizes in a manner analogous to Szekely's experiments with real flocks. To do this, one computes optimal decisions for a certain set of parameters, then modifies the parameters and recomputes the optimal decisions.

Table II shows the results of such computer experiments, using the time independent decisions. In these experiments, the ease of finding food is changed by changing  $\varepsilon$ , the size of food found is changed by changing  $Y$ , the risk of predation and the costs of foraging are changed by changing  $\beta$  and the  $as$ , respectively.

For example, an increase in the overall availability of food can be caused by either changing  $Y$  or changing  $\varepsilon$ . This leads to larger foraging groups for divisible resources and may lead to smaller flocks for indivisible resources. An increase in predation risk leads to an increase in

flock size except for cases in which reserves are nearly at the critical level and an increase in the energetic costs of foraging causes a reduction in flock size.

The value of  $\lambda(n)$  chosen for these computations causes  $\lambda(n)Y/n$  to be a decreasing function of  $n$ . Experiments were also conducted with a functional form for  $\lambda(n)$ , such that  $r(n)$  peaked at  $n=4$ . There is little difference in the optimal group sizes. For example, for divisible resources, the stationary optimal flock sizes are 3, 3 and 6 for  $x=3, 6$  and 10 and for indivisible resources the stationary optimal flock sizes are 1, 1 and 5 for  $x=3, 6$  and 10. This suggests that while the form of  $\lambda(n)/n$  is important for flock size arguments based solely on mean feeding rates (e.g. Clark & Mangel 1984, 1986), it is less important when a more unified approach, which includes predation and physiological state, is taken. Finally, if there is no predation pressure ( $\beta(n)=0$ ), the birds will forage individually when resources are indivisible and will have slight shifts or no shifts in flock size when resources are divisible. That is, even if predation is absent, the reduction in variance in food intake obtained by flocking provides an evolutionary advantage for flocking.

### AN OPTIMAL CALLER

Next consider a model for the experiments of Elgar. In this case, birds forage individually and when they find resources, determine whether to call for other birds. To highlight the call/do not call decision after food is found, I assume that there is no predation while searching for food, but only while feeding (this assumption is discussed in the last section). If the distinguished bird finds food and calls, then a fixed number ( $n$ ) of other individuals join it. I assume that the optimal caller does not consider the discoveries or decisions of other birds (that they need not join when another individual calls or that they will call when finding food) when the fitness function and calling decisions are determined. That is, the optimal caller makes its decisions on the assumption that  $n$  other birds will always join when it calls and does not consider calling activities by other birds. Thus, the model does not involve a dynamic game; the model treated in the next section does.

For divisible resources, the fitness function satisfies the equation

$$F(x, t, T) = \begin{array}{l} \text{Does not find food} \\ (1 - \lambda)F(x', t + 1, T) \\ \text{Finds food} \quad \text{Does not call} \\ + \lambda \max \{ (1 - \beta(1))F(x'', t + 1, T); \\ \quad \text{Calls} \\ (1 - \beta(n + 1)/n + 1)F(x''', t + 1, T) \} \end{array} \quad (11)$$

In this equation,  $x' = \text{chop}(ax - a_0; x_c, x_{\text{cap}}]$ ,  $x'' = \text{chop}(ax - a_0 + Y; x_c, x_{\text{cap}}]$  and  $x''' = \text{chop}(ax - a_0 + Y/n + 1; x_c, x_{\text{cap}}]$ . The three terms on the right-hand side of equation (11) correspond to (1) not finding food at all, in which case the bird continues foraging with a decremented value of reserves; (2) finding food but not calling in which case if the bird survives predation it begins the next period with a higher level of reserves; and (3) finding food and calling, in which case the bird survives predation with a higher probability but starts the next period with a smaller increment in reserves.

If resources are indivisible, it is likely that the finder has an advantage over other birds in actually obtaining the resource. Modelling this advantage can be done by a suitable choice of  $p_g(n)$ ; for example

$$p_g(n) = (1/(n + 1))^\gamma \quad (12)$$

In this equation,  $1/(n + 1)$  is the uniform probability that the finder would acquire the resource ( $n$  additional birds join the finder, hence the  $n + 1$ ) and  $\gamma$  is a parameter, with  $0 < \gamma \leq 1$ . If  $\gamma = 1$ , the  $p_g(n)$  corresponds to uniform probabilities of acquiring the resource and as  $\gamma$  decreases, the finder has a higher and higher probability of acquiring the resource. The parameter  $\gamma$  is a measure of the 'finder's advantage'. In this case, the equation that  $F(x, t, T)$  satisfies is

$$F(x, t, T) = \begin{array}{l} (1 - \lambda)F(x', t + 1, T) \\ + \lambda \max \{ (1 - \beta(1))F(x'', t + 1, T); \\ \quad \text{Acquires resource} \\ (1 - \beta(n + 1)/n + 1)\{p_g(n)F(x''', t + 1, T) \\ \quad \text{Does not acquire resource} \\ + (1 - p_g(n))F(x', t + 1, T)\} \} \end{array} \quad (13)$$

In both equations (11) and (13), the decision to call or not occurs after food is found. Thus, in the absence of predation, there is no fitness advantage to calling. The situation here is thus different from the situation in which flocks are formed before foraging occurs.

As equations (11, 13) are solved, we obtain a calling threshold denoted by  $x_{\text{call}}$  with the property

**Table III.** Threshold for calling (optimal decision is not to call if resources are found when reserves are below the threshold)

Case	Threshold for	
	Divisible resources	Indivisible resources
Base	3	4
$n \times 2$	4	4
$n \times 1/2$	3	4
$\varepsilon \times 2$	2	3
$\varepsilon \times 1/2$	6	6
$Y \times 2$	2	4
$Y \times 1/2$	4	4
$n \times 2$ and $Y \times 4$	2	4
$\beta \times 2$	3	4

$n$  = number of conspecifics joining upon calling.

that the optimal decision is not to call if reserves are below the threshold. Table III shows the results of computations for the base case (parameters  $x_c = 1$ ,  $\varepsilon = 2$ ,  $n = 10$ ,  $a = 0.5$ ,  $a_0 = 0.5$ ,  $x_{cap} = 10$ ,  $Y = 7$ ,  $\gamma = 1$  and  $T = 20$ ) and a number of cases in which parameters are changed.

Note the following. First, for both divisible and indivisible resources there is a range of the state variable in which calling is optimal. The range is larger (the threshold is smaller) for divisible resources. This agrees with Elgar's experimental results in which birds called for both kinds of resources, but with higher frequency on divisible resources. The threshold is most sensitive to the rate of finding food and the size of the food found ( $\varepsilon$  and  $Y$ , respectively) and less sensitive to values of  $n$  or  $\beta$ , at least for the parameters chosen here. This result is consistent with observations.

### THE STRATEGIC CALLER

When modelling the fitness of the strategic caller, we must consider the discoveries and decisions of other birds, in addition to the distinguished bird. This can be done in the following way. Let

$$p_c = \Pr\{\text{another bird calls if it finds food}\} \quad (14)$$

$$p_j = \Pr\{\text{one of the other } n \text{ birds joins if a call occurs}\} \quad (15)$$

Assume that in each period, each of the  $n = 1$  birds in the group can find at most one food item, that no discoveries occur simultaneously, and that the

**Table IV.** Threshold for calling by the strategic caller

Case	Threshold for	
	Divisible resources	Indivisible resources
Base	2	5
$n \times 1/2$	2	5
$\varepsilon \times 2$	2	3
$\varepsilon \times 1/2$	3	7
$Y \times 2$	2	5
$\beta \times 2$	2	4
$\beta \times 1/2$	1	5
$a \times 2$	2	6
$\gamma \times 2$	1	4

period is sufficiently long that all food items found can be consumed.

The equation for  $F(x, t, T)$  is analogous to (11) or (13), only more complicated because the behaviour of other birds must be considered. First, the distinguished bird may not find food. However, any number  $j$  of the other  $n$  birds may find food;  $k$  of the  $j$  finders may call and each time a bird calls,  $m$  of the remaining  $n - 1$  birds (other than the distinguished individual) may join. The probabilities  $\lambda$ ,  $P_c$  and  $P_j$  are used to characterize the binomial distributions for the number of other birds that find resources, that call if they find resources, and that join if a call occurs. Each time a call occurs, the distinguished individual has the choice of joining and attempting to feed (with concomitant risk of predation) or not joining. If the distinguished bird discovers food, then it has the option of calling or not calling; all of the events that happen to other birds still occur. For the case of divisible resources, when  $m$  other birds and the distinguished bird join the caller, the resource is shared by  $m + 2$  birds. For the case of indivisible resources, when  $m$  other birds and the distinguished bird join the caller, there is a contest for the resource. The calling bird has probability  $p_s(m + 2)$  of obtaining the resource, and the distinguished bird (if it is not calling) has probability  $\{1 - p_s(m + 2)\}/(m + 1)$  of obtaining the resource.

Table IV shows results for computations with these parameters:  $\varepsilon = 0.1$ ,  $n = 9$ ,  $x_c = 1$ ,  $x_{cap} = 10$ ,  $a = 0.95$ ,  $a_0 = 0.2$ ,  $\beta(n) = 0.002$ ,  $T = 13$ ,  $Y = 7$ ,  $\gamma = 1$ ,  $p_c = 0.3$  and  $p_j = 1$ . Taking the decisions of other birds into account leads to results that are even closer to those observed by Elgar: for divisible resources, the birds will essentially always call, but for indivisible resources the frequency of calling

will be much less. The results presented in Table IV also suggest a number of experiments. For example, for indivisible resources, as the ease of finding food increases we predict the calling will increase.

There is, however, one caveat that must be discussed with this model. The calling and joining probabilities should be, in fact, decision variables. Thus, they depend upon the state of the bird and the value of  $t$  and should rightfully be denoted by  $p_c(x, t)$  and  $p_j(x, t)$ . In that case, the appropriate way to treat fully the behaviour of other birds is not to fix the calling and joining probabilities, but instead to determine them as part of the computation. This leads to a dynamic game (see chapter 9 of Mangel & Clark 1988) in which the distinguished bird plays the role of the 'mutant' (Maynard Smith 1982) in a game against the field. The evolutionarily stable strategies would now be  $p_c^*(x, t)$  and  $p_j^*(x, t)$ . Mangel & Clark (1988, chapter 9) and Houston & McNamara (1988) describe iterative procedures for determining the dynamic evolutionarily stable strategies. These will not be developed here, since the main insights concerning the nature of flocking in relation to food and predation have already been obtained.

## DISCUSSION

By using dynamic, state variable modelling, one is able to develop a unified treatment of flocking behaviour that takes both starvation risk and predation risk into account, through a common fitness measure. The theoretical results show, for example, that flocking may be advantageous in terms of Darwinian fitness even when predation is absent and why individuals will call to share divisible resources but not call to share indivisible resources. A general result is that the fitness for birds foraging on divisible resources is higher (sometimes only slightly, sometimes considerably) than the fitness of birds foraging on indivisible resources.

The theory also leads to a number of explicit predictions, which can be generalized from flocks to foraging groups.

(1) In general, foraging groups will be larger towards the end of the day than in the middle of the day. The size of groups at the start of the day will depend upon the overnight dynamics of energy reserves.

(2) A comparative study of group foraging would show, all other factors being equal, group foraging

to be more prevalent in species exploiting divisible resources.

(3) When groups are formed before foraging occurs, an increase in the energetic value of forage, the rate at which food is found, or the risk of predation will typically increase the size of foraging groups if resources are divisible. An increase in energetic costs of foraging will typically decrease foraging group size. All of these effects are more pronounced for divisible resources than for indivisible resources.

(4) When groups are formed after food is found, by action of the individual finding food, there exists a threshold for calling in the sense that the individual will not call if its reserves are below this threshold. Such a threshold exists for both divisible and indivisible resources, with the threshold larger for divisible resources. Thus, in general, one predicts a higher frequency of calling when groups forage for divisible resources. An increase (decrease) in the rate of finding food typically decreases (increases) the threshold for calling and thus will increase the rate of calling. An increase (decrease) in the energetic value of food will typically decrease (increase) the threshold. Once again, these effects are more pronounced for divisible than indivisible resources.

(5) If predation occurs only while eating, and not while searching, one predicts that the individuals will search alone and call only after finding food. On the other hand, if predation also occurs during search, there will be selection pressure for group searching. In general, an increase in predation risk will lead to larger groups, except for cases in which energetic reserves are close to the critical starvation level.

(5) A finder's advantage will increase the frequency of calling after food is found. Although not explicitly modelled here, for the case in which groups are formed before foraging occurs, a finder's advantage would correspond to a larger share of the resource for the individual finding the food. I hypothesize that this would lead to larger foraging groups, but the theoretical details still need to be worked out.

The theoretical results suggest that in addition to measuring responses of flock size to increases in food or predator presence, we should be measuring the probability of finding food  $\lambda(n)$ , the probability of predation  $\beta(n)$  and the finder's advantage  $p_g(n)$  for birds in flocks of size  $n$ .

Two extensions of the theory are the following. Birds in flocks might receive unequal shares of the



resources not because of finder's effects but because of dominance relations (see Caraco 1987 for a treatment). The models developed here could easily be extended to include two types of birds, say dominant and subordinate, in flocks and to develop the decision for the distinguished bird on the basis of the flock composition. Second, by using forward iteration or Monte Carlo simulation (Mangel & Clark 1988), it is possible to follow the distribution of flocks over time, say 90 days in the winter. This gives predictions that could be matched more directly with experimental results. That is, rather than studying the optimal decisions, one studies the results of those decisions.

One question unresolved by this paper, and nearly all other theoretical ones on flocking, is the mechanism of flock formation. That is, imagine a collection of  $N$  birds. The  $i$ th bird will have an optimal flock size  $n_i(x, t)$  that it should join as a function of reserves  $x$  and time  $t$  in the winter. The dynamics of flock formation involve the question of how those  $N$  birds, each with its own optimal flock size, form and adjust flocks in response to their needs and the behaviour of others. This remains an important open question.

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