The Evolutionary Advantages of Group Foraging

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The relationship between the evolutionary fitness of individual foragers and the size of foraging groups is investigated by means of a series of simple mathematical models. Two alternative formulations of the contribution of foraging to fitness are considered, namely average feeding rate and probability of survival. The competitive aspects of group interaction are also considered, as are questions pertaining to the use of information. The latter leads to the concept of Behaviorally Robust Strategies. © 1986 Academic Press, Inc.

1. INTRODUCTION

The ecological literature reports numerous field and experimental studies of the foraging behavior of animal groups, including—to mention only a few—birds (Tolman and Wilson, 1965; Cody, 1971; Austin and Smith, 1972; Krebs *et al.*, 1972; Ward and Zahavi, 1973; Pulliam, 1973; Grieg-Smith, 1978; Pulliam *et al.*, 1982; Krebs and McCleery, 1984), ants (Bernstein, 1975), lions (Schaller, 1972; Caraco and Wolf, 1975), fish (Pitcher *et al.*, 1982; Magurran and Pitcher, 1983), bats (Howell, 1979), and humans (Orbach, 1977; Smith, 1981). Two general explanations have been suggested for the main evolutionary advantages of group foraging: (i) increased vigilance and protection against predators, and (ii) improved use of information in the presence of scarce, patchily distributed forage. Other advantages considered important in certain cases include (iii) increased ability to capture or subdue prey, (iv) more effective defense of resource supply, and (v) increased efficiency in the exploitation of

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depletable foraging. General reviews of the topic have been given by Bertram (1978), Pulliam and Caraco (1984), and Slobodchikoff (1984).

The ways in which group membership may aid the individual in detecting, avoiding, or deterring predators are well understood, and have been subject to careful analysis (Brock and Riffenburgh, 1963; Hamilton, 1971; Bertram, 1978; Pulliam and Millikan, 1982; Caraco and Pulliam, 1984). The mechanisms by means of which group foraging may lead to increased or more efficient feeding, however, are perhaps less obvious, since they depend on stochastic and uncertain elements in the foraging environment. For example, it is often asserted that group foraging can increase the average feeding rates of individuals whenever forage is scarce and patchily distributed, but both simulation studies (Thompson et al., 1974) and analytic models (Caraco, 1981) have failed to display such an effect. Under certain circumstances, however, group foraging can increase average feeding rates (Pulliam and Millikan, 1982; Clark and Mangel, 1984). Moreover, group foraging may increase survival probabilities, not by increasing average feeding rates, but by decreasing their variance (Thompson et al., 1974; Clark and Mangel, 1984). Alternatively, when food is scarce, foragers may optimize their chances of survival by maximizing variance (Caraco, 1981; Stephens and Charnov, 1982; Houston and McNamara, 1982).

An important aspect of group foraging behavior that until recently has largely been overlooked concerns the competitive interaction between individual group members. For example, the argument that evolution should tend to produce foraging groups of "optimal" size is seen, upon reflection, to depend tacitly upon an assumption of group selection. As shown recently by Sibly (1983), Clark and Mangel (1984), Pulliam and Caraco (1984), and Slobodchikoff (1984), in fact "overflocking" is normally the evolutionarily stable strategy. Various field observations support this prediction (see Section 5), but experimental verifications does not appear to have been attempted.

Many investigators have observed that animals in groups find and consume food faster than lone individuals (see Section 5), and this has often been uncritically interpreted as demonstrating an advantage of group foraging. The economic theory of common-property resources, however, suggests that the phenomenon may be the result of a competitive scramble (Gordon, 1954; Clark, 1980). Both overflocking and overintensive feeding activity within flocks can be predicted on the basis of theory of evolutionary games (Maynard Smith, 1982).

The purpose of this paper, then, is to reconsider all of these issues in a methodical fashion, using a series of deliberately simple models, most of which could be elaborated in useful ways. Section 2 deals with the question of what determines the actual size of foraging groups. Sections 3 and 4

investigate the relationship between the size of a foraging group and individual fitness—a complex relationship that depends on many environmental factors. Finally, Section 5 is devoted to critical reviews of several published empirical studies of group foraging. Here we discuss the concept of Behaviorially Robust Strategies.

2. Determinants of Group Size

Let $\phi(n)$ denote the fitness of an individual foraging in a group of size n. For the present we assume that there is no social order within the group (see Section 3), so that all members experience the same fitness. We also abstract from any specific definition of the term "fitness" (this question is also taken up in Section 3), assuming simply that fitness can be quantified as a nonnegative real number. We assume that individuals have evolved so as to attempt to maximize their fitness in any given situation, but we recognize that this attempt may involve social conflict; group formation and behavior are the result of individuals decisions, but what one individual does depends on what others are doing (Maynard Smith, 1982).

Figure 1 shows four conceivable shapes for fitness "curves" $\phi(n)$: (A) decreasing, (B) increasing, (C) and (D) peaked with $\phi(\infty) > \phi(1)$ and
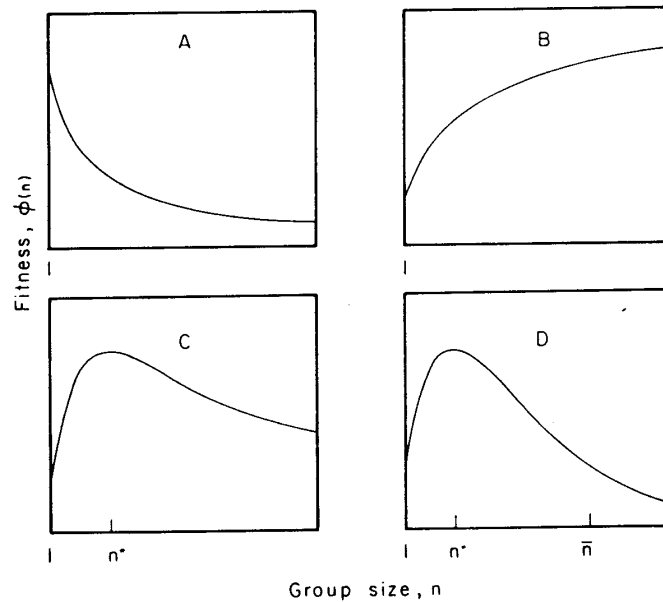
Fig. 1. Four types of fitness "curves" $\phi(n)$: (A) decreasing, (B) increasing, (C) peaked with $\phi(\infty) > \phi(1)$, (D) peaked with $\phi(\infty) < \phi(1)$.

$\phi(\infty) < \phi(1)$, respectively [it is customary and convenient to depict the sequence $\phi(n)$ as if it were a continuous function of the continuous variable n; the fact that n is actually integral has a slight and obvious effect of the ensuing arguments]. In Section 3 we will discuss circumstances giving rise to fitness curves having these various shapes. Here we are concerned with the equilibrium size $n = \bar{n}$. Most earlier authors (see Section 5) had tacitly assumed that evolution should result in optimally sized foraging groups ($\bar{n} = n^*$), but it has been noted independently by Schoener (1971), Sibly (1983), Clark and Mangel (1984), Pulliam and Caraco (1984), and Slobodchikoff (1984) that this assumption is not generally valid because of the *competitive* aspects of group foraging.

The *optimal* group size ($n = n^*$) is defined as that which maximizes individual fitness[1]:

$$\phi(n^*) = \max_{n \geq 1} \phi(n) \tag{2.1}$$

The *equilibrium* group size $n = \bar{n}$, on the other hand, is determined by the condition that

$$\phi(\bar{n}) = \phi(1) \tag{2.2}$$

unless $\phi(n) > \phi(1)$ for all $n \leq N$, in which case $\bar{n} = N$, the total population size. Briefly, the argument behind this conclusion is this (see Fig. 1D): consider an existing group of size $n < \bar{n}$. Then since $\phi(n) > \phi(1)$, a newly arriving individual will do better by joining the group than by foraging alone, even though when $n > n^*$ the fitness of the group is decreased by the addition of the new member. When n exceeds $\bar{n}$ a new arrival does best by feeding alone. More detailed discussions of the dynamics of group formation appear in the references noted above; see also Giraldeau and Gillis (1985).

In Section 5 we report on published field studies which support the prediction that $\bar{n} > n^*$. The authors of these studies were not aware of the prediction, and appear to have been taken aback by their findings. In one case at least (lions: Caraco and Wolf, 1975), the observed group sizes even exceeded $\bar{n}$. The reasons for this outcome remain somewhat obscure, but the two-person-game model of Clark and Mangel (1984), in which foragers "horn in" on each others' food discoveries, shows that groups for which $n > \bar{n}$ may be evolutionarily stable.

In cases where $\phi(n^*) \gg \phi(\bar{n})$ the equilibrium group size $\bar{n}$ is severely suboptimal. The question then arises whether any type of selection pressure would tend to counteract the tendency towards oversized foraging groups. For this to occur, group members would be required to expel intruders, and strategic considerations would be involved in the decisions of

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[1] Here we suppose that the *total* population size N is given, and the foraging decision consists of selecting the size of separate foraging groups which do not compete with one another.

individuals to participate in group defense. Such considerations are beyond the scope of the present paper (one example is discussed in Section 5); intuitively we expect that unless intruders are easily deterred, group-size defense would only be a stable strategy for kinship groups. On the other hand, the optimal size for kinship groups is obviously larger than the individual optimum (Rodman, 1981). (Dominance patterns may also affect group size; we discuss this briefly in Section 3.)

To conclude this brief section, we wish to comment upon the group foraging model discussed by Pulliam and Caraco (1984), which is based on biological assumptions which are quite different from those of our model. Pulliam and Caraco (1984, Fig. 5.2) consider a fixed population of N foragers deciding how to distribute themselves among two (generally, m) patches of forage. The individual fitness for n_i foragers on patch i is given by a function $W_i(n_i)$. The equilibrium distribution is Fretwell's (1972) "ideal free distribution," determined by the equations

$$W_i(\bar{n}_i) = W_j(\bar{n}_j); \qquad \sum \bar{n}_i = N.$$

Clearly some or all of the patches may become "overpopulated" in the sense that $\bar{n}_i > n_i^*$ where n_i^* maximizes $W_i(n_i)$.

Note, however, that with N fixed, the ideal free distribution *is* Pareto optimal: no alternative distribution can increase the fitness of one individual without decreasing the fitness of at least one other individual. Only a decrease in total population size N can reduce "overflocking" in this model.

The situation modeled by Clark and Mangel (1984) (see also Section 3 following) is quite different. In our model, increases in fitness result from increased search efficiency in groups (depletion of the resource is not included in either model). This increase in efficiency, however, is dissipated by overflocking. The equilibrium solution[2] $n_i = \bar{n}$, $\sum n_i = N$ is *not* Pareto optimal: the fitness of all individuals would be increased (for types C and D) if smaller foraging groups were formed. A welfare economist would describe the phenomenon in terms of "crowding externalities" (Pigou, 1946).

3. GROUP SIZE AND AVERAGE AND AVERAGE FEEDING RATE

We now consider the relationships between the size n of foraging groups and individual fitness $\phi(n)$. In order to model this relationship we must define fitness in operational terms. A standard definition, which underlies most of classical foraging theory, is that fitness from foraging is given by

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[2] These conditions can be satisfied approximately, by adjusting the number of foraging groups, if $N \gg \bar{n}$—see Clark and Mangel (1984, p. 631).

the average net rate of food, or caloric intake, while foraging (e.g., Krebs, 1978, p. 24). The behavior of foragers should then be predictable on the basis of the hypothesis that they attempt to maximize this net feeding rate. The energy maximization hypothesis can be justified on the basis of more general evolutionary models, during periods when the forager's energy reserves are low (Mangel and Clark, 1986).

Our task in this section, therefore, is to analyze the effects of group foraging on the average net feeding rate $\phi(n)$. An alternative definition of fitness, leading to different predictions, will be discussed in the following section.

An Elementary Search Model

Let $\phi(n)$ be the average individual feeding rate of foraging groups of size n. At first we ignore dominance effects, and assume that $\phi(n)$ is the same for all members of the group. The simplest possible model (Clark and Mangel, 1984) then assumes that forage occurs in patches of given size B, which are located by (Poisson) random search. The n foragers search independently and share equally each patch found. If λ denotes the individual Poisson search rate (expected number of patches located per hour of searching), then the group rate is $n\lambda$. Similarly, if τ denotes the time required for an individual to consume a patch, then the time for a group of size n to consume a patch is τ/n. Applying the renewal theorem (Karlin and Taylor, 1977) we obtain

$$\phi(n) = \frac{B/n}{\tau/n + 1/n\lambda} = \frac{B}{\tau + 1/\lambda}. \tag{3.1}$$

Thus $\phi(n) = \phi(1)$ for all n, and feeding rate is independent of group size.

In this model, foraging groups of size n locate patches at n times the individual rate, but since each patch is divided among the n group members, net feeding rate is unchanged. This result was also derived by computer simulation by Thompson *et al.* (1974), and analytically by Mangel and Plant (1984), who noted that the *variance* in individual feeding rate was reduced as n increased; we discuss this phenomenon in Section 4.

The numerator of the middle expression in Eq. (3.1) equals the forage per individual and the denominator equals handling time plus search time. If any of these three terms depends upon n in a form other than $1/n$, then $\phi(n)$ may be nonconstant. We will now consider the influence on $\phi(n)$ of the following aspects of group foraging:

(i)   interference in search,   (v)   ephemerality of patches,

(ii) communication problems,   (vi) learning,

(iii) nonuniform patch size or quality,   (vii) dominance effects.

(iv) satiation of foragers,

Interference

The assumption that n foragers search n times as efficiently as a single forager, while remaining sufficiently close together to share equally each patch found, is obviously increasingly unrealistic for large n. A decline in group search efficiency implies that the rate $n\lambda$ should be replaced by $n\lambda(n)$ where $\lambda(n)$ is a decreasing function of n [but $n\lambda(n)$ is nondecreasing]. Similarly, interference in feeding implies that the time to consume a patch is $\tau(n)/n$ with $\tau(n)$ an increasing function of n [but $\tau(n)/n$ nonincreasing]. The resulting feeding rate

$$\phi(n) = \frac{B}{\tau(n) + 1/\lambda(n)} \tag{3.2}$$

then becomes a decreasing function of n—i.e., type A. The effect of interference is to decrease individual average feeding rates.

Communication

The basic model assumes that information generated by group search is communicated to all members of the foraging group, who are then able to feed equally on discovered patches. Such an assumption is clearly realistic only for small n. Imperfect communication for large n implies that the overall effective search rate $n\lambda(n)$ increases less rapidly than n, having the same effect on $\phi(n)$ as nonindependent search.

Nonuniform Patches: Learning

The problem of assessing the quality of a given patch, and deciding when to abandon one patch and resume search for a new patch, has been studied in detail from the viewpoint of an individual forager (Charnov, 1976; Oaten, 1977; Krebs, 1978; Green, 1980; Iwasa *et al.*, 1981; McNamara, 1982), but not in terms of foraging group size. We can anticipate that groups of size n are able to estimate patch quality n times as rapidly (at best) as individual foragers, with an overall effect on $\phi(n)$ similar to the basic search model.

In Clark and Mangel (1984), for example, we considered the case in which the Poisson search parameter λ was a random variable having a gamma distribution with parameters v and α. If k items of forage are discovered by n individuals in search time t, then the posterior distribution on λ is also a gamma distribution, with updated parameters $v + k$ and $\alpha + nt$.

As another example, imagine an insectivorous bird feeding on insect larvae which occur on certain trees or shrubs—the patches. The location of such patches can be treated as known, but the *quality* of a given patch will be undertain to the forager until some time has been spent sampling it. For example, the patch may already have been depleted by other foragers.

More explicitly, assume that patches are identical, except that some have been depleted; the fraction of depleted patches, p, is known to the forager. Also assume a Poisson search process within a nondepleted patch, with search rate λ, the same for all such patches. The forager therefore has a prior distribution for λ:

$$\Pr\{\lambda = 0\} = p, \qquad \Pr\{\lambda = \lambda_1\} = 1 - p. \tag{3.3}$$

If n foragers search a nondepleted patch independently, then the probability of encountering no prey in time t is $e^{-n\lambda_1 t}$; as soon as one prey is encountered the patch is known to be productive, and is methodically gleaned for a fixed time t_1.

From Bayes' formula, the posterior distribution for λ is

$$\Pr(\lambda = 0 \mid \text{no prey encountered in time } t) = \frac{p}{p + (1 - p)\,e^{-n\lambda_1 t}}. \tag{3.4}$$

Suppose that foragers leave the patch when the posterior probability that it is a depleted patch reaches a certain level $p^* > p$. [The optimal value of p^* could be determined by the method of Green (1980). In a subsequent paper, we plan to provide a more complete discussion on mechanisms for evaluating p and p^*.] Then the "giving up time" t_n^* for a group of n foragers is obtained from Eq. (3.4):

$$t_n^* = \frac{1}{n\lambda_1} \ln \left\{ \frac{p^*(1 - p)}{p(1 - p^*)} \right\}. \tag{3.5}$$

A group of size n is able to estimate patch quality n times as fast as a single forager: $t_n^* = t_1^*/n$.

The average feeding rate can now be calculated (see the Appendix) as

$$\phi(n) = \frac{B(1 - p/p^*)}{n t_s(n) + C} \tag{3.6}$$

where

$$C = p t_1^*/p^* + (1 - p/p^*)\, t_e + \frac{1}{\lambda_1} \int_0^{\lambda_1 t_1^*} u e^{-u}\, du \tag{3.7}$$

where $t_s(n)$ is the time required to locate a new patch, and t_e is the time required for one forager to consume B.

If $t_s(n) \propto 1/n$, then $\phi(n)$ is again constant. However, in the case that the location of patches is known, $t_s(n)$ can be assumed constant and $\phi(n)$ thus becomes a decreasing function of n (Type A).

Satiation

The models discussed so far all indicate that group foraging either does not affect, or else reduces individual average feeding rates. The benefits of more frequent food discovery are at least balanced by having to share patches. These models, however, are based on the tacit assumption that the forager has infinite capacity. We now describe three possible mechanisms that may affect patch sharing and lead to *increased* feeding rates for groups of foragers. The first is satiation (Clark and Mangel, 1984).

Let C denote the feeding capacity of an individual forager. Assume that the forager leaves the patch when satiated, and resumes searching after a resting time proportional to its degree of satiation. If $m = B/C$ denotes the number of "meals" per patch, then

$$\phi(n) = \frac{C \min(1, m/n)}{(\tau + \tau_1) \min(1, m/n) + 1/n\lambda}$$

$$= \frac{C}{\tau + \tau_1 + 1/(\lambda \min(n, m))} \qquad (3.8)$$

where τ is the time to eat a full meal and τ_1 is the resting time when completely satiated.

The feeding rate $\phi(n)$ now becomes an increasing function of n for $n < m$, and $\phi(n) = \text{constant}$ for $n \geq m$. If m, the number of meals per patch, is large, the improvement from group foraging can be significant. For example, suppose $m = 100$, $\tau = 15$ min, and $\lambda = 1$ patch per hour. Then Eq. (3.8) gives $\phi(1) = 0.8$ meals per hour and $\phi(n) = 4$ meals per hour for $n \geq 100$.

By combining the effects of satiation and interference we obtain the general equation

$$\phi(n) = \frac{C}{\tau_1(n) + 1/(\lambda(n) \min(m, n))} \qquad (3.9)$$

where $\tau_1(n) = \tau(n) + \tau_1$ is the total "handling time." This curve has a peak at $n = n^*$ with $1 \leq n^* \leq m$, and is a type C or D curve (Fig. 1) if either $\tau(n)$ increases or $\lambda(n)$ decreases with n.

Ephemeral Patches

The following model of group foraging for ephemeral patches is an elaboration of a model suggested by Pulliam and Millikan (1982); see also Caraco and Pulliam (1984).

Assume Poisson search for patches, which are of fixed size B, and also

assume deterministic depletion of each patch by a "thinning" process of the form

$$\frac{dX}{dt} = -\alpha nX, \qquad t \geq 0$$

$$X(0) = B$$

(3.10)

where the constant α represents the proportion of the patch consumed per unit time, per individual. (Alternative depletion models give similar results.) If the group leaves the patch and resumes searching after time T, then the average individual feeding rate is given by

$$\phi(n, T) = \frac{(1 - e^{-\alpha nT}) B/n}{T + T_1/n}$$

$$= \frac{(1 - e^{-\alpha nT}) B}{T_1 + nT}$$

(3.11)

where $T_1 = 1/\lambda$ is the average time for an individual to locate a patch. Next, assume that the flock forages optimally, choosing $T = T^*(n)$ so as to maximize $\phi(n, T)$.[3] Observe that only the product nT appears in (3.11). Thus, we can consider a function $\psi(u)$ defined by

$$\psi(u) = \frac{1 - e^{-\alpha u}}{T_1 + u}$$

and let u^* maximize $\psi(u)$ over $u \geq 0$. Then

$$\phi(n) = \max_{T \geq 0} \phi(n, T) = B \max_{u \geq 0} \psi(u) = B\psi(u^*).$$

(3.12)

Thus, $T^*(n) = u^*/n$ is adjusted according to group size, and the resulting individual feeding rate $\phi(n)$ is independent of group size n.

But now suppose patches are ephemeral, and vanish suddenly after time T_0 (example: patches are located at daybreak and vanish at nightfall, or vice versa). The optimal feeding time per patch is now characterized by the problem

$$\phi(n) = \max_{0 \leq T \leq T_0} \phi(n, T)$$

$$= \max_{0 \leq u \leq nT_0} B\psi(u)$$

$$= \begin{cases} B\psi(nT_0) & \text{if } nT_0 < u^* \\ B\psi(u^*) & \text{if } nT_0 \geq u^*. \end{cases}$$

(3.13)

Thus $\phi(n)$ is increasing for $n \leq n_0 = u^*T_0$, and $\phi(n) = \text{constant}$ for $n \geq n_0$.

[3] Optimizing the time T does not involve any obvious competitive interaction between group members; individuals will presumably leave a given patch when it appears "exhausted."

As a numerical illustration, let $\alpha = 0.001/\text{day}$, $\lambda = 0.01/\text{day}$ ($T_1 = 100$ days), and $T_0 = 1$ day—the individual consumes 0.001 patch per day, and would only have a 1% chance of locating a patch per day; patches have a lifespan of 1 day. Then $n_0 = 416$ increases the average daily food intake by a factor of 66.6 relative to individual foraging. Similar results are obtained for other parameter values.

In general, the benefits of group foraging for ephemeral patches increase with the size of the patch relative to individual capacity, and with the search time required to locate patches. [A rough approximation for u^* in Eq. (3.12) is $u^* \approx \sqrt{2T_1/\alpha}$. Hence $n_0 \approx (\sqrt{2T_1/\alpha})/T_0$.]

Since $\phi(n)$ remains constant for $n \geq n_0$, i.e., ϕ is of type B, the theory of Section 2 predicts that arbitrarily large foraging groups would be observed under the present assumptions. As with the basic model, however, interference and communication problems would be expected to reduce $\phi(n)$ for large n, leading to a type C or D fitness curve, and a corresponding finite equilibrium group size.

Pulliam and Millikan (1982) assert that ephemerality of patches is the only circumstance under which group foraging would result in increased individual feeding rates, and that this would occur only when patches were extremely ephemeral. The latter claim is not made quantitatively; however, our numerical example suggests clearly that many observed occurrences of group foraging might well be encompassed by the ephemerality model. The behavior of vultures is one obvious candidate: carcasses are large and ephemeral, and by their soaring behavior vultures are able to keep large areas under observation, and to communicate discoveries effectively, if not deliberately. Another example involves fishing boats that search for schools of fish which aggregate during daylight and disperse during night time (Mangel and Beder, 1985). (For a further discussion of fishing boats, see Section 5.)

While not identical, the satiation and ephemerality models are obviously related. The assumption that the satiated forager leaves the patch, and later resumes searching, means that patches are ephemeral from his viewpoint. If the satiated forager is able to stay in the patch until hungry again, or if it can remember and return to the patch without searching, then the advantage of group foraging disappears. Satiation and ephemerality have a similar effect on $\phi(n)$ in Eq. (3.1): food intake per individual per patch exceeds B/n for small n.

Learning

In the basic model, increases in foraging group size result in increased search efficiency, but this is just balanced by decreased individual forage per patch. In the satiation and ephemerality models, individual forage per

patch does not decrease as rapidly as $1/n$, so that average individual feeding rates can increase with n.

In these models the information obtained by searching for forage is evanescent, and does not assist future search. In practice, searchers may learn something of lasting value. For example, in experimental feeding studies of great tits (*Parus major*) Krebs *et al.* (1972) found that the birds quickly learned from each other which types of container contained food. Such habitat "sampling" may also occur in the wild.

The following simple model illustrates the effect of such learning on individual feeding rates. Consider two "habitats" H_1 and H_2, containing randomly (Poisson) distributed forage items with means densities λ_1 and λ_2 respectively. The actual values of λ_1 and λ_2 are initially unknown, but the foragers have prior distributions $f_i(\lambda_i)$ for these values. Following Mangel and Clark (1983), we adopt the gamma distribution for these priors, and to simplify the calculations we will suppose that the prior distributions are the same for both habitats:

$$f_i(\lambda_i) = \gamma(\lambda_i; v, \alpha)$$

$$= \frac{e^{-\alpha\lambda_i}\alpha^v\lambda_i^{v-1}}{\Gamma(v)}. \tag{3.14}$$

This density has mean $\bar{\lambda}_i = v/\alpha$ and variance $\sigma_i^2 = v/\alpha^2$. (The use of the gamma prior distribution is arbitrary, and is chosen to simplify the calculations. We do not expect that the qualitative nature of the results would be affected by changing the form of the prior distribution.)

Assume independent search and perfect communication, as before. The foraging group searches both habitats, thereby obtaining updated estimates of λ_1, λ_2. If k_i foragers search H_i for time t_i and locate n_i food items, then the posterior distribution for λ_i is

$$f_i(\lambda_i \mid n_i) = \gamma(\lambda_i; n_i + v, \alpha + k_i t_i) \tag{3.15}$$

so that the updated estimate of the mean of λ_i is

$$\lambda_i' = \frac{v + n_i}{\alpha + k_i t_i} \tag{3.16}$$

Since it is assumed that λ_1 and λ_2 have the same distribution, a maximum amount of information will be obtained if the initial search effort is split evenly between H_1 and H_2. Thus we set $k_1 = k_2 = k = N/2$ where N is the total group size and $t_1 = t_2 = t$. The prior expected individual forage intake per unit time for the postsampling period is then given by

$$V = \sum_{n_1=0}^{\infty} \sum_{n_2=0}^{\infty} \Pr\{n_1\} \Pr\{n_2\} \max\left(\frac{v + n_1}{\alpha + kt}, \frac{v + n_2}{\alpha + kt}\right). \tag{3.17}$$

This formulation assumes no depletion of the habitat [see Mangel and Clark (1983) for equations pertaining to optimal search with depletion and nonsymmetric prior distributions]. In Eq. (3.17), $\Pr\{n_i\}$ denotes the prior probability of locating n_i food items on H_i during the sampling period:

$$\Pr\{n\} = \frac{(kt)^n}{n!} \frac{\alpha^v}{(\alpha + kt)^{n+v}} \frac{\Gamma(v+n)}{\Gamma(v)} \tag{3.18}$$

The sum in Eq. (3.17) must be calculated numerically. Utilizing the symmetry involved, we can express this sum as

$$V = c \sum_{n=0}^{\infty} p_n q_n \tag{3.19}$$

where

$$c = \frac{\alpha^{2v}}{(\alpha + kt)^{2v+1}}, \qquad x = \frac{kt}{\alpha + kt}$$

$$p_0 = v, \qquad p_n = \frac{v+n}{n} p_{n-1} x$$

$$q_0 = 1, \qquad q_n = q_{n-1} + \left(\frac{1}{v+n-1} + \frac{x}{n}\right) p_{n-1}. \tag{3.20}$$

Let T_{max} denote the total available feeding time. Assume sampling occurs for an initial period of length t after which all time is spent foraging in the patch with greater posterior expectation. The optimal sampling time t^* maximizes

$$V_{tot} = \frac{v}{\alpha} t + V(T_{max} - t) \tag{3.21}$$

where V, given by Eq. (3.19), depends on t. Table I shows the corresponding feeding rate $\phi = V_{tot}/T_{max}$ and the optimal group search time t^*, as functions of group size n. Parameter values are $\lambda = v/\alpha = 1.0$ item/min and $T_{max} = 10$ min. With no learning, the expected feeding rate would be 1.0 item per minute.

The relative effectiveness of sampling and learning depends on the initial uncertainty, as represented by the prior coefficient of variation, $CV = 1/\sqrt{v}$. For example, a lone forager can increase its expected intake by 27% by sampling, if $CV = 100\%$, or by 53% if $CV = 200\%$. For a group of size 50, these figures increase to 46 and 73%, respectively.

If T_{max} is increased, the benefits of sampling are further increased, but group sampling becomes relatively less beneficial. The reason for this is

TABLE I

Maximum Expected Individual Feeding Rate ϕ and Optimal Search Time t^*, as Functions of Group Size n, for Two Values of the Prior Coefficient of Variation CV

	CV = 1.0		CV = 2.0	
n	t^* (min)	ϕ (min^{-1})	t^* (min)	ϕ (min^{-1})
1	2.3	1.27	1.6	1.53
2	1.8	1.32	1.2	1.59
10	0.9	1.41	0.5	1.68
20	0.7	1.43	0.4	1.71
50	0.4	1.46	0.2	1.73

clear: with a long time horizon the individual can afford to do his own sampling, at least if the objective is to maximize average feeding rate over the period. The exact effect of increasing T_{max} is confounded by the other parameters in the problem and further discussion will appear elsewhere.

Dominance

In the basic model, information and food sharing balance out to provide no net change in individual feeding rate. A dominant group member, however, obtains more than $1/n$ of the food discovered by the group (Caraco, 1981). In combination with other factors affecting the individual feeding rate in groups, dominance will obviously enhance the feeding rate of dominant members while reducing that of subordinates. Thus dominance has the effect of increasing the tendency toward group foraging, while at the same time reducing the equilibrium size of foraging groups, relative to the case without dominance.

4. THE PROBABILITY OF SURVIVAL

In the previous section we have followed the early tradition of optimal foraging theory in equating fitness with average feeding rate. Many authors have noted, however, that this concept overlooks various important evolutionary aspects of foraging behavior. For example, Caraco (1981), Stephens (1981), and Stephens and Charnov (1982) have shown that under conditions of food scarcity, a forager may maximize its probability of survival by adopting a risk-prone feeding strategy with high variance, and possibly submaximal mean. Such a result—when desperate, gamble—cannot even be understood on the basis of the average rate criterion.

Let $f(X; \mu, \sigma)$ denote the probability density function for food intake during a given period, where μ and σ^2 denote mean and variance, respec-

tively. (Higher moments could conceivably be involved in survival, but we do not discuss this possibility.) If R denotes the forager's minimal food requirement for the given period, then the probability of survival for the period is

$$\Pr(X \geqslant R) = \int_R^\infty f(x; \mu, \sigma) \, dx = 1 - F(R; \mu, \sigma) \tag{4.1}$$

where F denotes the cumulative distribution of f.

Suppose that the forager's strategy choices are specified in terms of a given mean-variance set Ω. The optimal strategy in terms of survival is then determined by the criterion

$$\underset{(\mu,\sigma)\in\Omega}{\text{minimize }} F(R; \mu, \sigma) \tag{4.2}$$

A geometrical solution to this elementary minimization problem was given by Stephens and Charnov (1982), for the case in which f is the normal distribution. The generalization to arbitrary distributions is straightforward.

For example, suppose that the forager's strategy choice consists of foraging alone, or joining a group of $n - 1$ other foragers. The set Ω then consists of two points (μ, σ) and (μ_n, σ_n). Figure 2 shows the set of all points (μ_n, σ_n), $n = 1, 2, 3, ...$, joined into an arc, for the case where the average individual feeding rate μ_n is type D. Thus μ_n first increases and then decreases; the variance σ_n^2 decreases monotonically with n.

The optimal and equilibrium group sizes can be obtained by the construction of Stephens and Charnov (1982). Under the normality assumption, the level contours of $F(R; \mu, \sigma)$ for fixed R are straight lines in the (μ, σ) plane passing through $(R, 0)$—see Fig. 2. The line meeting Ω and
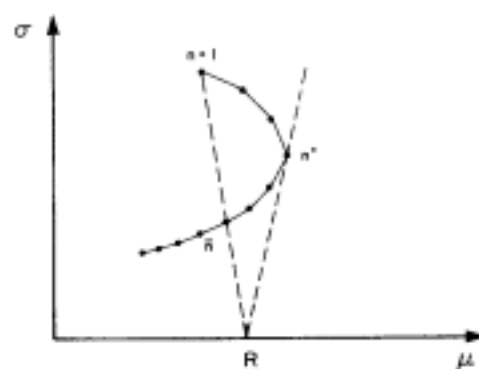

FIG. 2. Optimal group size n^* and equilibrium group size $\bar{n}$ for the case in which $\phi(n)$ equals the probability of survival.

with smallest possible slope determines the optimal group size n^* and corresponding mean and variance μ^*, σ^*. The equilibrium group size $\bar{n}$ is on the level contour passing through $n = 1$.

The qualitative dependence of n^* and $\bar{n}$ on R can be read from Fig. 2—both decrease with increasing R, indicating the increase in risk proneness associated with increased food deficit (Caraco, 1981). (Note that we can now have $\bar{n} > n^*$ even for type A average feeding rate curves.)

These qualitative predictions remain valid for arbitrary distributions f, provided only that

$$\frac{\partial F(R; \mu, \sigma)}{\partial \mu} < 0, \tag{4.3}$$

i.e., provided that an increase in expected food intake implies a decrease in the risk of starvation.

An alternative model of group foraging, which is more closely related to the models of Section 3, is the following. Assume that an individual forager captures food items according to a Poisson process with parameter λ, and assume zero handling time. The probability of consuming k food items in time t is then given by

$$p(k, \lambda) = \frac{(\lambda t)^k}{k!} e^{-\lambda t}, \qquad k = 0, 1, 2, \dots . \tag{4.4}$$

The mean and variance of this distribution are both equal to λt.

If a group of n foragers encounters food items at the rate $n\lambda$, then the probability that the group finds k items in time t is

$$p(k, n\lambda) = \frac{(n\lambda t)^k}{k!} e^{-n\lambda t}, \qquad k = 0, 1, 2, \dots . \tag{4.5}$$

If food items are shared equally, the individual's mean food consumption is again λt, but the variance is $\lambda t / n$. The cumulative distribution functions for $n = 1$ and $n = 5$ are illustrated in Fig. 3. It is immediately clear from Fig. 3 that the forager's probability of survival is maximized by foraging alone if $R > \lambda t$, and by group foraging if $R < \lambda t$. (The result must be modified if λ in fact depends upon n.)

Sequential Decisions

The foregoing models assume that the forager's probability of survival is determined by a single decision, whereas in reality an entire sequence of decisions will be involved, with the outcome of one decision influencing future decisions in a feedback fashion. Dynamic foraging models have been discussed by Katz (1974), Craig *et al.* (1979), Houston and
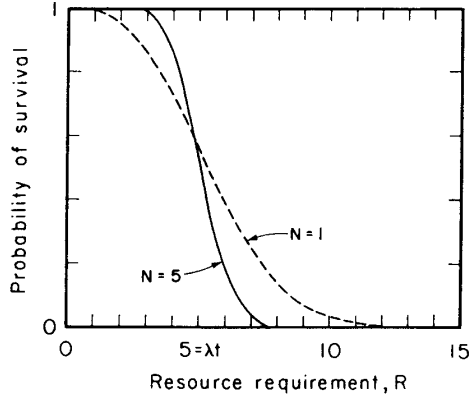
FIG. 3. Probability of survival for Poisson search model, as a function of resource requirement R, for an individual forager and for a group of five foragers (λt = expected forage discovery = 5.0).

McNamara (1982), and McNamara and Houston (1982). A general sequential model of foraging behavior would allow for alternative behavior—sleeping, breeding, territorial defence, etc. We develop a class of such models in a forthcoming paper (Mangel and Clark, 1986). Here we discuss briefly a simple sequential decision model of group foraging.

Let $J_i(R)$ denote the maximum probability of survival, i.e., using an optimal strategy in each period, given that i periods remain and that the food deficit at the outset of the first of these periods is R. Then one obtains

$$J_{i+1}(R) = \max_{(\mu,\sigma)\in\Omega} \int_0^\infty J_i(R-x) f(x; \mu, \sigma)\, dx \tag{4.6}$$

with

$$J_0(R) = \begin{cases} 0 & R > 0 \\ 1 & R \leqslant 0 \end{cases} \tag{4.7}$$

where $f(x; \mu, \sigma)$ is the probability density function for food intake x per period. Equations (4.6) and (4.7) determine an inductive procedure (dynamic programming) for determining $J_N(R)$ and the optimal strategy (μ_N^*, σ_N^*).

To prove (4.6), suppose that some strategy $(\mu, \sigma) \in \Omega$ is chosen in the first period, when $i+1$ periods remain. Food intake x will occur with probability density $f(x; \mu, \sigma)$. The conditional deficit at the beginning of the next period will be $R - x$. Thus, for this strategy choice we have

$$\Pr(\text{survival} \mid x) = J_i(R - x) \tag{4.8}$$

so that

$$\text{Pr(survival)} = \int_0^{\infty} J_i(R - x) f(x; \mu, \sigma)\, dx. \qquad (4.9)$$

By maximizing over $(\mu, \sigma) \in \Omega$, we obtain Eq. (4.6). The initial condition (4.7) is evident.

Note in particular that

$$J_1(R) = \max_{(\mu,\sigma) \in \Omega} \int_0^{\infty} J_0(R - x) f(x; \mu, \sigma)\, dx$$

$$= \max \int_R^{\infty} f(x; \mu, \sigma)\, dx$$

$$= 1 - \min F(R; \mu, \sigma) \qquad (4.10)$$

which is precisely the result from the one-period problem. For $N > 1$ the solution must be obtained numerically. The behavior of the model for large N has been analyzed by Houston and McNamara (1982), who show that the optimal policy is to minimize variance if expected discoveries exceed R and vice versa. [Note that this is the same as the short-term (one-period) optimal strategy.] In terms of group foraging, the resulting prediction is that animals are more likely to forage in groups when forage is abundant than when it is scarce, other things being equal. But since in most situations both the mean and variance of the feeding rate will depend on group size, the prediction must be treated with caution.

5. Case Studies

In this final section we review several published case studies of group foraging. We hope thereby to demonstrate that the comprehensive theory presented in this paper can lead to the formation of more rigorous hypotheses and improved explanations concerning the causes and effects of group foraging.

A common class of errors encountered in discussions of group foraging is based on the misconception that individual fitness should be optimized by group behavior. As noted in Section 2, this assumption completely overlooks the fact that intragroup competition may be as important as cooperation, if not more so, as a determinant of group behavior. The most direct form of this error is the prediction that observed group size should optimize individual fitness, but other instances also occur.

Suppose, for example, that observations show that certain animals foraging in groups discover food patches more rapidly, or experience higher

feeding rates, than individuals. It does not automatically follow that group foraging is beneficial. When foraging together, individuals may be forced to exert excess effort, both in searching and in feeding, in order to obtain their share of the available forage. This is simply another manifestation of the well known dynamics of common-property resource exploitation.

As a simplistic illustration, imagine two birds feeding in a linear patch of forage, beginning at one end. The faster moving bird will get to eat all the forage, the other nothing. If they start at opposite ends, each bird's share will be proportional to his speed (ever try sharing a milkshake?). Hence both birds will be forced to eat as rapidly as possible—at least, assuming that " property rights" cannot be established by initial "agreement" on the division of territory. Clearly the fact that the two birds are feeding, or searching, faster than when foraging alone cannot be taken as evidence that group foraging increases individual fitness.

The extent to which the predictions of optimality models can be tested has been widely discussed (see, for example Krebs et al., 1983; Krebs and McCleery, 1984). It would seem that the ideal test would be a controlled experiment, in which the assumptions underlying the model could be closely simulated, and extraneous variables could be eliminated. Yet perhaps not surprisingly, animals in experimental situations often behave in ways that do not seem to fit the theory very well.

It is our view that one of the main reasons that animals often fail to behave "according to theory" can be described in terms of what we call Behaviorally Robust Strategies (BRSs). By this term we mean strategies that are operational for the animal, and which perform satisfactorily in terms of expected fitness in the presence of all the fluctuations and uncertainties that the animal can expect to face in nature. Considered in isolation, such a strategy may not actually be optimal in any specific situation. Any strategy observed, whether in nature or under experimental conditions, must be a BRS. [The term Rules of Thumb (ROT) has been employed to describe an analogous concept; see Krebs et al. (1983). We prefer the term BRS for its greater generality, and also for its avoidance of an anthropomorphic cliché.]

This principle has two immediate corollaries, the first being that an animal cannot be expected to perform well in an experiment that is far removed from situations it can expect to encounter in nature. This is obvious and needs no discussion—even though animals do continue to amaze us with their problem solving capabilities.

The second corollary is more subtle. Some of the information known to the experimenter and apparently available to the subject may in fact not be useful to the subject because such information would never, or almost never, be encountered under natural conditions. Animals are not adapted to laboratories. By similar token, an animal subject will usually have no

way of knowing that the variability always to be expected in nature has been eliminated by experimental design. Consequently some residue of uncertainty-coping behavior—probing, sampling, watching—can be expected to be present even when the experimenter knows that it is "useless."

Goldfish and Minnows

In a series of papers (Pitcher *et al.*, 1982, 1983; Magurran and Pitcher, 1983; Pitcher and Magurran, 1983) the effects of group size on the foraging behavior of goldfish and minnows were studied.

Pitcher *et al.* (1982) demonstrate that fish in larger shoals find food faster. The decrease in mean search time with shoal size is hyperbolic. This observation is consistent with independent searching, since with independent searching, the mean time for a shoal of fish to discover a patch of food is proportional to the reciprocal of shoal size.[4] The authors also point out that such behavior indicates that the fish can recognize when a neighbor has found a patch, which they then attempt to share.

Pitcher and Magurran (1983) investigated the relationship between shoal size and the proportion of time that a marked individual spent foraging. For both minnows and goldfish the foraging time increased markedly with shoal size up to 20 fish (although with goldfish it leveled out at 12 fish). The authors argue that this phenomenon can be attributed to the need for increased vigilance against predators when the prey are in small groups: "Fish in small shoals make longer and more frequent visits to cover, shorter and less frequent visits to the food patch, and dart and turn more while swimming" (Pitcher, and Magurran, 1983, p. 151). No actual of simulated predators were present in these experiments, however (but see Magurran and Pitcher, 1983).

The authors reject the hypothesis that fish in large shoals spend more time foraging because of increased competition, on the basis that the experimental design eliminated the possibility of food depletion during the experiments (Pitcher and Magurran, 1983, p. 152). From the BRS viewpoint, the question might be raised whether the fish were aware of the fact that they could ignore depletion for the duration of the experiment, while not being aware of the absence of predators. Either the competition or the predation hypothesis (or both) seems sufficient explanation for the experimental observations, particularly if one assumes that fish have evolved to deal with natural rather than laboratory environments.

A simple model of the response of foraging shoals to predation can be formulated as follows. Let t denote the proportion of time devoted to

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[4] For Poisson search, the expected time to locate a patch is $1/\lambda$; if k fish search independently λ is replaced by $k\lambda$.

hiding from predators, and $1 - t$ the proportion spent foraging (other types of behavior are ignored). Let $g(t)$ denote the probability of obtaining enough food over a specified time period; clearly $g'(t) \leqslant 0$, $g(1) = 0$. Let $h_n(t)$ be the probability of being eaten by a predator during the period, for an individual member of a shoal of size n. A natural choice for $h_n(t)$ is

$$h_n(t) = h_1(t)/n$$

where $h_1'(t) \leqslant 0$, $h_1(1) = 0$.

Let $t = t_n^*$ maximize the probability of survival $p_n(t) = g(t)(1 - h_n(t))$. With the additional (weak) assumption that $p_1(t)$ is convex, it is easy to see that t_n^* is a decreasing function of n, with $t_n^* \to 0$ as $n \to \infty$. Fish in larger shoals should spend a higher proportion of their time feeding because of the reduced chance of any given individual being eaten. (The model does not reflect the vigilance aspect of shoaling. If vigilance were included, $h_n(t)$ could decrease more rapidly than $1/n$.)

Pitcher and Magurran (1983) next performed an experiment in which they let fish "adjust" to a tank with a number of patches of high, medium, or low food content. They then introduced a "misinformed" fish (i.e., one who had adjusted to a different environment) into the tank and studied the behavior of the shoals. The observations that we wish to discuss are these:

(1) The presence of misinformed fish increased the time that informed fish spent on poorer patches.

(2) Groups of four misinformed and one informed fish determined the best patch faster than a pair consisting of one misinformed and one informed fish. The authors found this puzzling, since in the first case the majority of the fish started with the wrong information.

(3) When all the fish were informed, "shoals of 2 made fewer and shorter visits [than larger shoals] to sample the medium and low-profitability food patches" (p. 552).

These observations can be interpreted using our theory as follows:

(1) The presence of misinformed and informed fish indicates a mixture of prior distributions. With such mixture of distributions, one would expect updating to be a much slower process.

(2) For Bayesian updating, the rate at which a prior distribution is updated is proportional to the rate of sampling (Clark and Mangel, 1984). Figure 4 of Pitcher and Magurran (1983) shows that a shoal of two fish took about 2.2 times longer than a shoal of five to update patch quality, compared to the value of 2.5 predicted by simple proportionality.

(3) According to Pitcher and Magurran (1983), "the precise reason for greater sampling [low profitability patches] remains obscure in this

experiment" (p. 554). The possibility of depletion and competition was ruled out on the grounds that "the amount of food set on the patches was much greater than could be eaten in 10 min, as determined in pilot experiments" (p. 553). But unless the fish are aware of this information (and evolved to utilize information of this nature), the BRS would clearly be for fish in larger shoals to expect more rapid patch depletion and to consider sampling other nearby patches. In order to determine whether to forage alone or with a shoal, each fish must continually estimate the feeding rate under both conditions. With larger shoals, the shoal feeding data in natural circumstances would change more rapidly, requiring greater effort in sampling.

Great Tits

In a study of the flocking behavior of great tits, Parus major, Krebs et al. (1972) reported that birds in groups of two found food faster than individuals, and that birds in groups of four found food faster than groups of two. A consistent observation reported in this paper was "horning in" on food discoveries: whenever one bird observed that another had found food, it immediately gave up searching and attempted to appropriate some of the other bird's food. This sharing of food discoveries is a feature of our group foraging models in Section 3 above, and was analyzed in terms of ESS in Clark and Mangel (1984). Krebs et al. (1972) attribute this behavior to "dominance" within the flock. We believe, however, that since horning in is the ESS, it is unnecessary to invoke the dominance effect.

Domestic Chicks

Tolman and Wilson (1965) and Tolman (1965) report experimental studies of the social feeding behavior of domestic chicks. These authors use the phrase "social facilitation" to describe the observation that chicks feed more rapidly in groups than alone. Table II shows the food consumption for 5-day-old chicks placed in a small enclosure for 1 h, as a function of the length of time the chicks were deprived of food prior to the experiment (Tolman and Wilson, 1965, Fig. 1). The separated pair of chicks was placed in adjacent enclosures separated by a plexiglass partition; paired chicks were placed in the same enclosure. No statistical significance separates pairs of numbers appearing below the dashed line in Table II.

From these and other data, Tolman and Wilson (1965) conclude that "social facilitation is the product of some specific kind of behavioral interaction" (p. 141). However, their only specific hypothesis concerning this interaction, which they call "emotion" (lone chicks feed slowly because isolation causes them to become emotional), is rejected on the experimental evidence. But in a subsequent paper it is concluded that "social facilitation [can] be accounted for by reduction of emotional behavior due to visual

TABLE II

Average Amount of Food Consumed per Chick (g)
in Tolman and Wilson's (1965) Feeding Experiments

Size of group	Deprivation time (h)			
	0	6	12	24
1	0.3	1.1	1.6	1.9
2 separated	0.3	1.0	1.4	1.8
2 paired	0.4	1.7	1.9	2.1
4	0.5	1.8	1.9	2.2
16	0.5	1.9	1.8	2.0

Note. All numbers below the dashed line are statistically indistinguishable.

presence of a companion" (Tolman, 1965, p. 495). The later experiments, however, involved only brief 10-min feeding periods; "with longer test periods which allow adaption,... a physical contact–behavioral interaction appears to be more pertinent" (Tolman, 1965, p. 495). No suggestion is made as to how physical contact "facilitates" feeding.

We believe that the experimental results can be interpreted in a different fashion by observing that eating faster in the presence of a companion is an ESS due to competition for the same resource. With such an interpretation, one would not expect any difference between groups of two, four, or sixteen. If the chicks in the separated case were able to recognize the plexiglass partition as preventing the other chick from horning in, then one would expect this case to be similar to isolates. This was the observation.

In order to model this strategic game in a simple way, let us assume that whenever it faces competition, the individual chick attempts to maximize its food intake, provided that it is sufficiently hungry.

If B denotes the total food available in a given "patch," and if f_i is the pecking rate of chick i, then the food intake of chick i is proportional to

$$\frac{f_i}{\sum f_j}$$

To maximize this, the chick uses the largest possible f_i, and this trivial solution is the ESS. Note that the prediction agrees closely with *all* the data presented by Tolman and Wilson (1965): under competitive conditions the chicks feed at approximately the rate that a starved lone chick does (Table II).

A lone chick that is a starved need not be concerned with total food intake, and can afford to consider both energetic costs and benefits. Any reasonable maximization model would qualitatively predict the first row of Table II. An experimental test of our hypothesis would consist of varying the size of the enclosure: we predict that the feeding rate of groups of chicks would decline as the enclosure size increases, perhaps with a threshold effect.

If our hypothesis is correct, a more appropriate phrase to describe the feeding behavior of chick groups might be "competitive interaction." It is worth noting that eating faster in the presence of a (real or imagined) companion does not imply more efficient foraging. Pecking at the maximum possible rate may be considerably less efficient in terms of costs and benefits than pecking at a more leisurely rate. The use of the term "social facilitation" seems to prejudge the issue; we would prefer the term "social interaction."

Bats

The foraging behavior of the nectivorous bat *Leptonycteris sanborni* Lydekker, feeding on desert agaves, *Agave palmeri* Engelm, in the Chiricahua mountains of Arizona, is described and analyzed by Howell (1979). These bats forage at night in flocks of 25 bats or more; the exact size of flocks could not be determined, but energetic calculations indicated that flocks larger than about 120 bats would fail to break even in terms of net energy intake while feeding.

Howell (1979) considers several possible explanations for the flock foraging behavior of these bats. The passive-aggregation and anti-predation hypotheses are rejected. Concerning feeding efficiency, the author is somewhat ambivalent, first stating that "the most robust advantage of flocking... is increased foraging efficiency. *Agave palmeri* is a spatially and temporally patchy resource.... Energy savings in initial search will accrue to flocking bats" (Howell, 1979, p. 37). But then Howell concedes that a hypothetical solitary territorial bat might well do as well as or better than a flock member. Hence "the most convincing argument deals with the ability of the coevolved system to persist" (Howell, 1979, p. 41).

Other suggested advantages of flocking are first that flocks exploit the agave resource in a more orderly "clean sweep" fashion (Cody, 1971), and second that communal roosting raises body temperatures and facilitates digestion. As noted in Section 2, however, the Cody hypothesis depends on a group-selection argument.

If we overlook the communal roosting argument, we are still left with explaining why bats join foraging groups rather than defending solitary agave territories, or foraging alone. A single agave plant provides sufficient nectar to feed one bat over a period of about 1 month (Howell, 1979,

p. 41), and a typical patch of agaves flowering simultaneously would feed several bats for a month. Aggregative response would then produce bat groups of some size, since an individual bat would not profit by defending a territory much larger than it needed. But then the common-property argument indicates that such groups would tend to increase beyond the capacity of the agave patch to support them for a full month. There is no reason to expect the resulting flocks to be of optimal size (although Howell asserts that they should be).

The theory of Section 3 indicates that individual feeding rates would not be increased by flocking of bats. Agave patches are not highly ephemeral (although individual panicles are so), and although individual bats quickly become satiated, they can and do frequently return to the same plant after resting.

Next let us consider the effect of flock foraging on the variance of individual bats' feeding rates. Agave patches last about 1 month each during the summer flowering season from June to September. Different patches in the Chiricahuas are separated by tens of kilometers (Howell, 1979, p. 37). A solitary bat would be forced to find a new patch each month (at least), and the expected length of flight required for this would be of the order of tens of kilometers.

Bats in flight have high metabolism rates, estimated by Howell (p. 33) at 0.13 kcal/km. When satiated with nectar, bats' stomachs carry about 2.8 kcal, so that a bat cannot expect to fly more than 22 km without "refueling." One role of flocks, then, may be to reduce the variance assocated with finding new patches of agave. The behavior of bat flocks searching for new agave patches has not been observed. Since flowering agaves emit a "batty odor" (Howell, 1979, p. 25), location may not be a random search process. Presumably flocks are more efficient searchers than individuals, but the mechanisms of search and communication remain to be investigated.

In summary, Howell (1979) is undoubtedly correct in claiming that a multitude of factors favor flocking of these bats. Added to the arguments put forth should be the possibility of reducing search time, and the likelihood that large forage patches attract several bats and may induce flocking, even overflocking. By producing large food supplies, agaves may be "exploiting" bat sociality mechanisms, inducing flocking behavior that maximizes the movement of bats and pollen between agave patches (Howell, 1979, p. 42).

Human Foragers

In this section, we will consider two types of human foragers: the tuna fishermen from San Diego, California, studied by Orbach (1977) and the Inuit (Canadian Eskimos) studied by Smith (1981). As Smith points out,

the two main reasons for group formation are information sharing and resource sharing.

The tuna men exhibit a highly developed form of information sharing in their "code groups." These are groups of vessels, sometimes linked by skipper kinship but often not, that share information about the location of good fishing sites. This information is transmitted through highly developed code schemes. The origin of these codes can be interpreted in terms of our theory as follows. Since tuna are highly migratory and there is considerable difficulty in finding them as well, tuna can be viewed as an ephemeral, patchy resource. Thus it is reasonable to assume that a type D curve is applicable, with $\bar{n} > n^*$. The code group represents a relatively costless way for the members of the group to keep group size closer to n^* than $\bar{n}$. This presumes, of course, that the members of the group can estimate n^*. We believe that it is certainly possible to estimate the relative sizes of $\bar{n}$ and n^*, simply on the basis of experience. The use of code groups is relatively costless bacause (1) the vessels already carry the requisite radio equipment needed for transmitting information, and (2) the codes can be established during times when the vessels are not at sea. The development of such code groups is completely consonant with our theory. Many other fishermen are known to employ codes and other strategies for protecting information.

The Inuit are resource sharers who form groups for the purpose of hunting various kinds of prey. These include seal, whale, caribou, fox, goose, duck, trout, and whitefish. Based on energetic considerations, that is kilocalories per kilogram of edible weight, Smith (1981) computed optimal group size under the assumption that a type D feeding curve is valid. The validity of a type D curve can be argued, although Smith does not do so, as follows. Capture rate should initially increase, but ultimately saturate with group size. The energy available to an individual in a group of size n, assuming no dominant members, is simply $1/n$ of the total energy available from the prey. Combining these two leads to a type D curve. Smith used energetic models to compute n^* for ten different types of hunts. His results are shown in Table III. According to Smith (1981, p. 60), in 4 out of these 10 cases the hypothesis that the most frequently occurring group size is the most efficient is supported by a statistical test. These are lake jigging, acean netting, jig/goose, and ptarmigan. Two cases, spring goose and beluga, are indeterminate, and in the remaining four cases the hypothesis was not supported.

To quote Smith (1981, p. 63), "it is evident that the present data do not provide overwhelming support for the general idea that group size will be tightly optimized to maximize individual energetic efficiency." Smith goes on to try to explain the failure of the simple hypothesis about maximizing individual energetics.

TABLE III

Group Sizes for Inuit Hunters

Hunt type (Sample size)	n^*	Mean group size	Most frequent group size in sample (%)
Lake jigging (60)	1	2.8	1 (42)
Ocean netting (69)	1	1.6	1 (67)
Jig/goose (25)	1	2.6	1 Not given
Spring goose (53)	3	2.4	1 Not given
Ptarmigan (27)	1	1.5	1 (64)
Lead/floe edge (54)	2	2.7	1 (41)
Breathing hole (19)	3	3.9	4 (84)
Canoe seal (36)	1	2.9	2–3 (69)
Beluga (6)	5–6	10.3	— Not given
Winter caribou (10)	6–7	4.0	3, 5 (Bimodal—30 each)

We believe, however, that the six cases in which Smith's hypothesis is not supported are consistent with equilibrium group sizes predicted at a level $\bar{n}$. One could, in fact, compute the energetic intake and see if the hypothesis $\phi(1) = \phi(\bar{n})$ is supported by the data that Smith provides. Furthermore, for the four cases in which the simple hypothesis is supported, one could ask if there are any social mechanisms that push group size from $\bar{n}$ to n^*. This could be a fruitful area for future anthropological research.

Finally, Smith mentions that in other studies of social predators such as hyenas (Kruuk, 1975), chimpanzees (Busse, 1978), and lions (Caraco and Wolf, 1975; also see Clark and Mangel, 1984) "confirmation has generally been no stronger than in the Inukjuamiut case" (Smith, 1981, p. 65). If one takes the broader view of foraging theory, as advocated in the present paper, many of these apparently contradictory results are more easily understood.

APPENDIX

The derivation of Eq. (3.7) proceeds as follows: by the renewal theorem, $\phi(n)$ can be expressed as the ratio of the expected individual food consumed per patch located divided by the expected time to locate, search, and consume the patch. The probability that a given patch is depleted is p. If the patch is not depleted its Poisson search parameter is $\lambda_1 > 0$. The probability that a good patch will yield no food encounters in time t_n^*, and thus be rejected, is

$$e^{-n\lambda_1 t_n^*} = e^{-\lambda_1 t_1^*} = \frac{1 - 1/p^*}{1 - 1/p} \tag{A1}$$

by Eq. (3.5). Hence the expected amount of food eaten per patch discovered, per individual, is

$$(1 - p)(1 - e^{-\lambda_1 t_1^*}) \cdot B/n = (1 - p/p^*) \cdot B/n. \tag{A2}$$

The expected time spent to decide whether a given patch is depleted can be written as

$$\bar{t} = t_n^* [\text{Pr(patch depleted)} + \text{Pr(patch not depleted, but rejected)}]$$

$$+ \int_0^{t_n^*} t \, \text{Pr(patch not depleted, and first encounter occurs in } t, t + dt)$$

$$= t_n^* [p + (1 - p) e^{-n\lambda_1 t_n^*}] + \int_0^{t_n^*} t e^{-n\lambda_1 t} n\lambda_1 \, dt$$

$$= \frac{pt_1^*}{p^* n} + \frac{1}{n\lambda_1} \int_0^{\lambda_1 t_1^*} u e^{-u} \, du. \tag{A3}$$

Finally, the expected time spent eating in a given patch is

$$\bar{t}_e = \text{Pr(patch not depleted or rejected)} \cdot t_e/n$$

$$= (1 - p/p^*) t_e/n \tag{A4}$$

by the same algebra as in (A3), where t_e is the time required for an individual to consume a whole patch.

The expected time required to locate a patch is denoted by $t_s(n)$, so that the average feeding rate can be expressed as

$$\phi(n) = \frac{(1 - p/p^*) B/n}{t_s(n) + \bar{t} + \bar{t}_e} \tag{A5}$$

and this agrees with Eq. (3.7).

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