PRODUCERS, SCROUNGERS, AND GROUP FORAGING

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Abstract.—We have developed a model that reconciles information-sharing and producer-scrounger models of group foraging. Our model includes producers, scroungers, and an opportunistic forager that can both produce and scrounge but with reduced efficiency. We show that these three strategies can coexist only in the unlikely case that the opportunist's loss in searching ability is exactly equal to its gain in scrounging ability. However, all pairs of strategies can coexist. Three parameters control the proportions of coexisting strategists: the degree of compatibility between the opportunist's producing and scrounging activities; the proportion of food patches that are shared with scrounging individuals; and the effective group size. When there is little incompatibility between producing and scrounging, opportunists will always be present, unless the producer is able to consume most of the patch without sharing. The opportunist strategy is always excluded when there is a high degree of incompatibility between producing and scrounging. We consider the organismal and ecological factors that are likely to affect all three parameters. Our model predicts that scrounging behavior is likely to be selected in a wide range of foraging groups and that it may impose a considerable cost on sociality.

When animals forage in groups, the food discoveries of a few can lead to the feeding of many. This almost inescapable consequence of the presence of others is one of the major characteristics of social foraging and can take many forms. It ranges from gleaning information concerning the kinds of places that are likely to contain food (Krebs et al. 1972; Rubenstein et al. 1977; Palameta 1989) to sharing patches discovered by others (Clark and Mangel 1984; Giraldeau 1984; Giraldeau and Lefebvre 1986; Giraldeau et al., in press) to outright expropriation of food from its finder, a phenomenon known as kleptoparasitism (Brockmann and Barnard 1979; Vollrath 1984). To predict the effects of group living on feeding behavior, as well as the selective pressures fostering and constraining group formation, it is important to understand when such exploitative relationships will occur and their consequences for the foraging rates of all the individuals involved.

Theoretical explorations of these questions have taken two approaches. One approach has examined how group size influences the rate of food discovery (Thompson et al. 1974; Pulliam and Millikan 1982; Clark and Mangel 1984) or success of prey capture (Packer and Ruttan 1988) for all group members. This approach has generated what we call "information-sharing" models, although in

some cases more than simply information is shared. These models are primarily concerned with the functional advantage of sociality. Clark and Mangel (1984) provide a typical information-sharing model. They elaborate a flocking game that assumes that all individuals in a group search independently while simultaneously observing one another. When a patch of food is located, all group members converge on the patch and feed. The model concludes that an individual often does better by joining a foraging group than by foraging alone, even when groups tend to be so large as to impose some "overflocking" costs to its members. Information-sharing models thus can predict group sizes and have given rise to concepts of optimal (Brown 1964; Caraco and Wolf 1975) and stable (Sibly 1983; Caraco and Pulliam 1984; Clark and Mangel 1984) group sizes.

The second approach is based on the observation that the widespread occurrence of interspecific kleptoparasitism (Brockmann and Barnard 1979; Vollrath 1984; Barnard and Thompson 1985) also applies at the intraspecific level (Barnard and Sibly 1981). These studies have used the theory of frequency-dependent games (Maynard Smith 1982) to ask whether it is possible to have stable mixtures of hosts ("producers") and parasites ("scroungers") (Barnard and Sibly 1981; Parker 1984a, 1984b; Sibly 1984). Unlike information-sharing models, the producer-scrounger model does not assume that all group members behave in the same way. Rather, some individuals specialize in producing and others in scrounging. The model posits a strong, negative frequency dependence on the scroungers' payoffs such that they do very well when rare but very poorly when common. Additionally, when they are rare, scroungers must do better than producers (Parker 1984a, 1984b) because scroungers can increase their foraging rate by using the group's corporate rate of producing while avoiding the costs of producing. When these conditions are met, the producer-scrounger model predicts that specialized producers and scroungers will coexist in stable equilibriums at that frequency of scroungers for which payoffs to both strategies are equal—a mixed evolutionarily stable state (ESS). Thus, individuals will be either pure producers or pure scroungers or will alternate between pure producing and pure scrounging at the ESS frequency.

The information-sharing and producer-scrounger models make radically different assumptions about an individual's foraging behavior. The information-sharing models assume that individuals can monitor the foraging activities of others without any decrement in their own individual rate of patch discovery. We call this the assumption of complete compatibility. The producer-scrounger model, on the other hand, assumes that a pure producer, or an individual playing producer on a given play of the game, cannot scrounge. Thus, the producer-scrounger model assumes, at least implicitly, complete incompatibility between the search for food patches and the exploitation of the discoveries of others.

These extreme assumptions of complete compatibility and complete incompatibility are unlikely to be entirely valid in any given situation. In fact, considerable evidence suggests that at least some intermediate degree of incompatibility may be more likely. For instance, there are many documented examples of the trade-offs between predator vigilance and feeding rate (Caraco 1979; Barnard 1980;

Bertram 1980; Caraco et al. 1980; Elgar et al. 1986). Similarly, there is evidence suggesting that individuals that specialize on one food type or foraging task out-perform those that do not specialize (Werner et al. 1981; Partridge and Green 1985, 1987; Templeton 1987; Laverty and Plowright 1988). The different techniques required to do well on different foraging tasks (Persson 1985), combined with the costs of switching between tasks (Murdoch 1969), will likely prevent the achievement of maximum foraging efficiency if these tasks are undertaken concurrently. This form of incompatibility, reflected by decreased performance, is also a well-studied human phenomenon in the cognitive-psychology literature, where it is referred to specifically as the "division of attention" (reviewed by Mackworth [1970]).

In addition to the problem of compatibility between the two foraging alternatives, it is important to understand how the costs of scrounging behavior will influence the evolution of group foraging. Information-sharing models have suggested that foraging in groups will not increase foraging rate over solitary foraging (Thompson et al. 1974; Pulliam and Millikan 1982; Caraco 1987). Others have proposed that group foraging may be stable even if it imposes some costs to its members relative to solitary foraging (Clark and Mangel 1984; Packer and Ruttan 1988). The producer-scrounger model has not dealt with the effect of scroungers on the average foraging rate of group members. This is because the model does not specify any effect of the scroungers on the payoffs to the producer strategy (Parker 1984b).

In this study we explore the consequences of a more realistic group-foraging model that deals explicitly with the potential incompatibility of producing and scrounging. We modify the producer-scrounger game by adding to it a third strategist, the "producer-scrounger opportunist" (henceforth called "opportunist"), which is borrowed from information-sharing models. The opportunist uses a search mode that permits it to search simultaneously for both producing and scrounging opportunities and exploit them as detected. Simultaneous search increases encounter rate with foraging situations, but incompatibility reduces the rate of detection of these encountered opportunities. The opportunist is therefore a pure strategy even though its food comes from both producing and scrounging. Our goal is to determine how the inclusion of such an opportunist strategist modifies the predictions of producer-scrounger and information-sharing models concerning the use of others' food discoveries. Specifically, we predict the ecological circumstances in which different combinations of the strategies are likely to evolve and coexist. Finally, we examine the consequences of the occurrence of scrounging individuals for the evolution of group foraging and sociality.

THE MODEL

Consider a group of animals foraging closely enough together so that for each individual there is a nonzero probability of detecting and participating in feeding when a food patch is located by another individual. Animals in the group use one of three strategies: producer, that is, searching for food for themselves and then

eating it; scrounger, that is, never searching for food but rather surveying the producers and always joining to consume part of each discovery; and opportunist, that is, searching for food and surveying the producers concurrently and feeding from both sources as detected. We assume for simplicity that each individual is a pure strategist, in that it uses only one of the three strategies described above and does not alternate between them. Because its feeding mode is conditional on what it detects, even though it "plays" only a single search strategy, the opportunist is somewhat similar to an "environmentally determined conditional strategy" such as "retaliator" in the hawk-dove model (Parker 1984*a*).

For a group of N individuals, we define the proportions of producers (p), of scroungers (q), and of opportunists (r), where $p + q + r = 1$. Let food occur in a limitless number of patches each containing F items. (Alternatively, patches could each consist of a single item divisible into F portions.) Suppose that patches are scarce so that search time is long relative to patch exploitation time. Thus, time spent in patches can be ignored in this analysis. On discovering a patch, an individual may eat some items before any scroungers and opportunists (henceforth collectively referred to as scrounging individuals) arrive. We call the number of items that the producer of a patch obtains for its exclusive use the "finder's advantage," a. The remainder, $A = F - a$, is divided equally among the producer and all scrounging individuals. We refer to the proportion of each patch that is eaten by the sum of these individuals as A/F, the "scroungers' share."

We assume that producers search independently and find patches at rate f. If c is the proportional ability of opportunists to detect a patch as compared to producers, then cf is the finding rate of opportunists. The rate of scrounging is set by the available number of discoveries, which is the number of discoveries by producers, pNf, plus the number by opportunists, $rcNf$. Opportunists, however, only detect a fraction (h) of those discoveries that scroungers detect. We assume that, in a given environment, the proportional searching ability, c, and the proportional scrounging ability, h, of an opportunist will be negatively related. Furthermore, when the opportunist performs only one of the alternative foraging roles, its ability equals that of the equivalent specialist; that is, when $h = 0$, $c = 1$, and vice versa. The functional relationship between h and c may vary with species (visual acuity, speed of movement, patch-detection technique, etc.) and with environment (patch visibility and size, prey reactions, distribution of conspecifics, etc.). Possible relationships are outlined in figure 1. When producing and scrounging are completely compatible, as is assumed in information-sharing models, c and h each take their maximal values of 1. For complete incompatibility, as is assumed in producer-scrounger models, only two conditions are possible: when $h = 0$ and $c = 1$, the opportunist is effectively a producer; and when $h = 1$ and $c = 0$, the opportunist is effectively a scrounger. In cases of partial compatibility, we consider three cases (fig. 1): "overcompensation," "undercompensation," and "exact compensation." Exact compensation means that any change in the opportunist's behavior that increases producing ability will result in an equal loss in its scrounging ability ($c + h = 1$). When overcompensation occurs, gains in c or h are greater than any losses in h or c, respectively ($c + h > 1$).

FIG. 1.—Possible relationships between the relative scrounging ability of an opportunist (h) and its relative producing ability (c). All relationships are bounded by two points of complete incompatibility; one is located in the upper, left-hand corner where $h = 1$ and $c = 0$, and the other in the lower, right-hand corner where $h = 0$ and $c = 1$. The diagonal linking these two points represents the line of exact compensation between the opportunist's relative producing and scrounging abilities ($c + h = 1$). Any line above this diagonal will necessarily be convex and represent an overcompensation ($c + h > 1$) of the producing and scrounging abilities. Any line below the diagonal will be concave and represent an undercompensation ($c + h < 1$) of the producing and scrounging abilities.

Conversely, undercompensation refers to the case in which gains are smaller than losses ($c + h < 1$).

On the basis of above definitions, we can calculate food intake, I, over some period of search time, T, for each of the strategists:

$$I_p = fT(a + A/n), \tag{1}$$

$$I_s = (p + rc)fNTA/n, \tag{2}$$

$$I_o = cfT(a + A/n) + h(p + rc)fNTA/n = cI_p + hI_s, \tag{3}$$

where I_p denotes intake by producers; I_s, by scroungers; I_o, by opportunists; and $n (= 1 + qN + rhN)$ is the number of animals that share a patch, once found. Note that this expression is precise only when a producer finds a patch. When an opportunist finds a patch, $n' = 1 + qN + h(rN - 1)$ should be used because the opportunist that has found the patch cannot also be counted as a scrounging individual. In large groups the difference between n and n' is negligible. We ignore it in our analyses. The difference between n' and n does not influence the main conclusions of this article. However, tests based on small groups should reevaluate predicted ESSs using n'.

Evaluating the change in food intake for each strategy, we differentiate equations (1), (2), and (3) with respect to p, q, or r while specifying which strategy is

replacing which other strategy. For example, to see the effect of scroungers replacing producers in a group of fixed size, we calculate dI_p/dq, dI_s/dq, and dI_o/dq for the case where $dp/dq = -1$ and $dr/dq = 0$. Under these conditions, $dI_p/dq < 0$, $dI_s/dq < 0$, and $dI_o/dq < 0$. Thus, all strategies suffer lost food intake when scroungers replace producers. This occurs because there are fewer patches found as the number of producers in the group declines, as is assumed in the producer-scrounger model (Barnard and Sibly 1981). Conversely, if producers were to replace scroungers in the group, food intake would increase for all three strategies since more producers in the group would find more patches.

When scroungers replace opportunists in a group of fixed size (i.e., $dr/dq = -1$, and $dp/dq = 0$), we calculate $dI_p/dq < 0$, $dI_s/dq < 0$, and $dI_o/dq < 0$. Again, food intake for all strategies declines as scroungers replace opportunists, which reduces the rate at which patches are found within the group. Conversely, when opportunists replace scroungers, food intake will increase for all three strategies.

When opportunists replace producers ($dp/dr = -1$ and $dq/dr = 0$), food intake decreases for all strategies: $dI_p/dr < 0$, $dI_s/dr < 0$, and $dI_o/dr < 0$. Conversely, if producers replaced opportunists, food intake would increase.

Food intake by scroungers and, to some extent, opportunists is frequency-dependent in two ways. First, as seen above, the patch-discovery rate of the group decreases as producers are replaced because there are fewer animals searching for food patches. Second, scrounging individuals (scroungers plus opportunists) obtain a smaller proportion of each patch found as their frequency increases because more animals share each patch. The food intake of a producing individual (either a producer or an opportunist) is frequency-dependent to a lesser extent. Increasing the frequencies of scrounging individuals increases the number of animals that share a patch. However, producing individuals, unlike scrounging individuals, are not affected by a reduction in the corporate patch-discovery rate of the producing individuals. The food intake of a producer declines because it is losing food to one or both scrounging strategies, but this decline is less rapid than that of the scrounging strategies. Ultimately, the scrounging strategies will do only as well as the producer and much worse than a solitary producer. Overall, benefits to all three strategies increase as producing individuals increase in frequency while benefits decrease as scrounging individuals increase.

Coexisting Strategies

Under what conditions can the alternative search strategists coexist? We take a game-theory approach to answering this question (Maynard Smith 1982). Stable, equilibrium coexistence will occur when food intake is equal among strategies and no single strategy can do better by modifying its frequency (Nash equilibrium).

First, we check whether the three strategists can coexist in stable equilibrium. If so, $I_p = I_s = I_o$, and, from equation (3) in the ESS,

$$I_p = cI_p + hI_p, \tag{4}$$

which, in turn, implies that $h + c = 1$. This means that the three strategies can coexist in stable equilibrium only if losses in searching ability are matched exactly

by gains in scrounging ability. This is the case of exact compensation (fig. 1). In this case the opportunist receives the same payoffs as a mixed strategist in the producer-scrounger game (Barnard and Sibly 1981). Any departure, however minute, from exact compensation will preclude equilibrium coexistence.

It remains possible, however, that the three strategies can coexist without a stable equilibrium (Maynard Smith 1982). To evaluate this possibility we must see whether each strategist can invade a group that is in stable equilibrium with respect to the other two strategies. Consider first the case of opportunists invading an equilibrium group of producers and scroungers. At equilibrium, $I_p = I_s$, so that equation (3) becomes $I_o = cI_p + hI_p = (h + c)I_p$. Thus, opportunists can invade an equilibrium group of producers and scroungers if and only if $h + c > 1$. When undercompensation occurs ($h + c < 1$) opportunists cannot invade. Now suppose that scroungers invade an equilibrium group of producers and opportunists. Since $I_p = I_o$, equation (3) reduces to $I_s = (1 - c)I_p/h$. Therefore, scroungers can invade an equilibrium group of producers and opportunists only when $h + c < 1$, the case of undercompensation. When overcompensation occurs, an equilibrium group of producers and opportunists resists invasion. The third case involves producers invading an equilibrium group of opportunists and scroungers. Since $I_o = I_s$, equation (3) becomes $I_p = I_s(1 - h)/c$. Thus, producers can invade an equilibrium group of opportunists and scroungers only when $h + c < 1$. When $h + c > 1$, an equilibrium group of opportunists and scroungers resists invasion.

Overall then, opportunists will not be part of an ESS if $h + c < 1$. Under this condition, they cannot invade an equilibrium population of producers and scroungers, but both producers and scroungers can invade equilibrium populations containing opportunists. When $h + c > 1$, opportunists can invade an equilibrium population of producers and scroungers and neither producers nor scroungers can invade equilibrium populations involving opportunists. Thus, a combination of producers and scroungers cannot form an ESS, but opportunists can coexist with either producers or scroungers in an ESS. Globally, coexistence of the three strategies is only possible if $c + h = 1$. We consider this to be unlikely, however, since even minor deviations from exact compensation will exclude at least one of the three strategies.

Generally, ESSs of this game will involve only one or two strategies. These strategies and their proportions in the group can be found by setting equations (1), (2), and (3) equal to each other, subject to the conditions that each p, q, and r must fall between 0 and 1. If $h + c < 1$, setting equation (1) equal to equation (2) shows that $p \geq 1$ when $A/F \leq 1/N$. When the scroungers' share is less than the proportion that each individual makes up of the group as a whole, the ESS is pure producer. For instance, in groups of two, the producer is stable as long as A/F is less than 0.5, or conversely, a is greater than $0.5F$. As group size increases, a pure-producer ESS will become less likely because producers must monopolize an ever-greater fraction of the patch to prevent scroungers from invading. A group of 10 producers, for instance, will be stable only if a exceeds $0.9F$.

When $A/F > 1/N$, scroungers can coexist with producers at ESS. Setting equa-

TABLE 1

PROPORTIONS p, q, AND r OF THE THREE STRATEGISTS, PRODUCER, SCROUNGER, AND OPPORTUNIST, AT ESS UNDER VARIOUS CONDITIONS

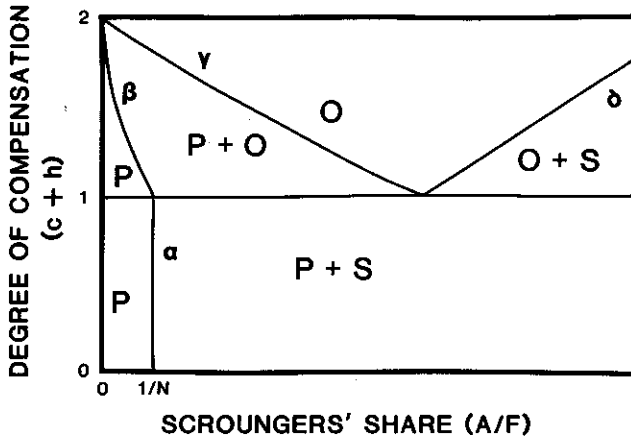| Conditions		ESS Proportions of Strategists		
$h + c$	A/F	p	q	r
<1	$\leq 1/N$	1	0	0
<1	$>1/N$	$1/N + a/F$	$A/F - 1/N$	0
>1	$\leq (1 - c)/(hN)$	1	0	0
>1	$\begin{array}{l}>(1 - c)/(hN) \\ <(1 - c)(1 + 1/(hN))\end{array}$	$1/(hN) + a/[F(1 - c)] - c/(1 - c)$	0	$A/[F(1 - c)] - 1/(hN)$
>1	$\begin{array}{l}\geq (1 - c)(1 + 1/(hN)) \\ \leq h + 1/N\end{array}$	0	0	1
>1	$>h + 1/N$	0	$[1/(1 - h)][(A/F) - (1/N) - h]$	$1/(1 - h)[(a/F) + (1/N)]$

Fig. 2.—Transition thresholds between various ESS combinations of the producer (P), scrounger (S), and opportunist (O) strategies as a function of the degree of compensation between an opportunist's producing and scrounging abilities $(c + h)$ and of the scroungers' share of each patch (A/F). The horizontal line at $c + h = 1$ depicts exact compensation between an opportunist's producing and scrounging abilities. Below this line no opportunists are expected at ESS. The producer ESS occupies a relatively small area to the left of $1/N$ when the scroungers' share is small, but the greater part of the area below the line of exact compensation is occupied by an ESS combination of producer and scrounger strategies. Above the line of exact compensation the opportunist strategy is prevalent. A producer ESS is possible at very small scroungers' shares, but its likelihood decreases as the extent of compensation approaches complete compatibility. An opportunist ESS occupies an increasingly larger area as compensation increases toward complete compatibility. Evolutionarily stable state combinations of producer and opportunist strategies occur for small scroungers' shares especially when compatibility barely exceeds exact compensation. Evolutionarily stable state combinations of opportunist and scrounger strategies are expected at large scroungers' shares. The equations for each threshold are as follows: for line α, $A/F = 1/N$; line β, $A/F = (1 - c)/(hN)$; line γ, $A/F = (1 - c)(1 + [1/(hN)])$; and line δ, $A/F = h + (1/N)$. The lines represented here are only some of the possible combinations depending on group size. Lines β and γ can vary in shape from linear to concave. Line δ can be linear, concave, or convex. Lines α and β will always meet at $c + h = 1$, as will lines γ and δ.

tion (1) equal to equation (2) shows that ESS proportions will be $p = a/F + 1/N$ and $q = A/F - 1/N$. The p in the group will increase as a increases and will decrease with larger group sizes. These are the only two ESSs possible when $h + c < 1$ since opportunists cannot be involved in an ESS and scroungers cannot survive alone.

A similar analysis for the condition $h + c > 1$ shows that there are four possible ESSs that depend on the values of A/F, N, c, and h (see table 1 for a summary of the conditions and their expected ESSs; see fig. 2 for a graphical illustration of one specific case). As A/F increases, the ESS changes from producer to producer and opportunist, to opportunist, and then to opportunist and scrounger. Increasing group size has the effect of lowering the transition thresholds between the mixtures of strategies, thus increasing the range of values of the scroungers' share over which scrounging individuals are expected. Increasing values of $c + h$ favor opportunists by (1) lowering the thresholds of the transition from producer

to producer and opportunist, and then to opportunist only and (2) raising the threshold of the transition from opportunist only to opportunist and scrounger. As h increases, the range of scroungers' shares that will favor the opportunist strategy is decreased by raising both the threshold of transition to producer and opportunist and the transition to opportunist and scrounger. In the extreme case of complete compatibility, $h + c = 2$, the ESS is opportunist alone regardless of the value of A/F.

When the ESS consists of two strategies, the proportions are affected similarly by the thresholds. The r in a mixture with producer is increased by N, A/F, h, and c. The r in a mixture with scrounger is decreased by A/F and N and increased by h.

The Cost of Social Foraging

Foraging rate under the conditions outlined here is constrained by rate of patch discovery, which in turn depends on the number of producing individuals in the group. The presence of scroungers will reduce total foraging rate in proportion to their frequency. Opportunists will reduce the average foraging rate of the group in proportion to their frequency and their relative inefficiency in producing food patches. In a mixture of producers and scroungers, the corporate rate of patch discovery will be pfN, compared with fN for producers alone. For example, using equations in table 1, in a group of 10 animals with an A/F of 0.9, we expect eight scroungers and two producers at ESS. The foraging rate of the individuals in this group will be only 20% of the rate observed in a group of 10 producers. In a mixture of producer and opportunist strategies in a group of 10 individuals with, say, an A/F of 0.25, $h = 0.8$, and $c = 0.6$, animals will feed at 80% of the rate of a group of pure producers. Whenever some animals exploit the finds of others, all members of the group do worse than if no exploitation had occurred. The almost inevitable spread of scrounging behavior within groups and its necessary lowering of average foraging rate may be considered a cost of group foraging.

DISCUSSION

Information-sharing models assume that all group members should both produce and scrounge (Thompson et al. 1974; Pulliam and Millikan 1982; Clark and Mangel 1984). The producer-scrounger model, on the other hand, assumes that individuals should specialize in either producing or scrounging at any one time (Barnard and Sibly 1981; Parker 1984a, 1984b). Our analysis, which takes into account factors such as the scroungers' share and the incompatibility between producing and scrounging activities, suggests that these assumptions are often unrealistic. According to our model, groups consisting solely of opportunist strategists, as assumed by the information-sharing models, should occur only when there is considerable overcompensation between producing and scrounging abilities. Moreover, mixtures of producer and scrounger strategies that are predicted by the conventional producer-scrounger model should occur only in situations of strong undercompensation. In most intermediate situations of incompatibility the opportunist strategy is expected to coexist with either the producer or the

Factors Influencing the Model's Parameters

To predict the frequency of occurrence of the different foraging strategies, it is important to understand the factors that are likely to lead to either under- or overcompensation. Situations in which the detection of either a producing or a scrounging opportunity requires merely short, well-spaced scans will probably lead to overcompensation. For instance, if patches, once discovered, are not depleted quickly, then a brief scan at infrequent intervals will be sufficient to achieve maximum detection probability (Pulliam 1973). The time between scans may thus be more profitably spent searching for producing opportunities. At the other extreme, if discovering food requires some form of long systematic search, as is involved with cryptic prey, then interruptions to scan for scrounging opportunities are likely to be costly (Lawrence 1985). In those situations we expect undercompensation, and producer and scrounger strategies will be favored over the opportunist.

Any factor that is likely to increase detectability of scrounging opportunities, be it active food calling (Elgar 1986) or conspicuous behavior that accompanies production of food (e.g., the long dive of a sea bird and the noise or smell of prey capture), is likely to favor overcompensation and the occurrence of opportunists. It is probably reasonable to assume, in addition, that, if different sensory modes are used when searching for prey and when monitoring others, the two activities should be considerably more compatible.

Another factor that is likely to be important in determining the extent of compensation is the transition time between activities. At one extreme it may only be the time necessary for the eyes to focus on a different point. At the other extreme it may involve physical displacement of an individual from one area where producing is likely to another where scrounging is facilitated. For instance, a ground-feeding animal foraging in dense undergrowth may need to move to higher places to scan for scrounging opportunities. The transition time will then reduce the opportunist's efficiency in both activities relative to the producer or scrounger strategies.

The extent of incompatibility between producing and scrounging activities may be reduced somewhat by modifications of an individual's foraging behavior. It is possible that opportunists that suffer undercompensation, for instance, may increase their searching efficiency by reducing the range of food types they include in their search set. Such a reduction in the search range could lead not only to an increased rate of producing but also to increased detection efficiency of scrounging opportunities. This kind of process could lead to the formation of a skill pool in which different individuals specialize in producing different subsets of the population diet while scrounging on all food types (Giraldeau 1984). There is some indirect evidence of the existence of skill pools (Giraldeau and Lefebvre 1986). If the opportunists did behave in such a way, they would be distinguished from the producer strategists by the narrower range of food items they discover. Other behavioral modifications to reduce incompatibility might include altering components of the foraging act (Lendrem 1984) or altering the type of prey that is selected (Lima 1987).

Factors that are likely to affect the scroungers' share include those parameters

scrounger strategy. The greater the extent of overcompensation, the greater the expected frequency of the opportunist strategy.

Most information-sharing models assume that the producer and the scrounging individuals share a food patch equally (i.e., no a; but see Caraco 1987). There is evidence, however, of an a when individuals share patches (Giraldeau et al., in press). Our model demonstrates that the a will have great importance in determining whether scrounging strategies will be selected. The model predicts that there exists a minimum threshold value A/F for which scrounging strategists are selected. As A/F increases, the frequency of either or both scrounging strategies in the group will increase. The kind of scrounging strategy that is favored, however, depends on the extent of compensation.

Except for the specific case of cooperative hunting (Packer and Ruttan 1988), information-sharing models do not predict any change in the frequency of producing and scrounging as group size increases. In the case of cooperative hunting, as group size increases, a "cheater" strategy somewhat similar to our opportunist is expected to be more common, although the problem of compatibility was not included in Packer and Ruttan's (1988) analysis. Barnard and Sibly (1981) predict that in most situations group size will have an effect on the stable frequencies of producer and scrounger strategies. Our model confirms this. It predicts that as group size increases, the frequency of the scrounger strategy should increase at a monotonically decreasing rate toward an asymptote of A/F.

Much of the distinctiveness of our model hinges on the existence of a third strategist, the opportunist, that is different from an individual adopting a mixed strategy of producer and scrounger. Current evidence does not allow us to distinguish between these two different strategies in empirical studies of group foraging. For instance, in the house sparrows for which the producer-scrounger model was first proposed, producers obtained 19.8%–38.3% of their food by scrounging while scroungers obtained 38.5%–48.8% of their food by producing (Barnard and Sibly 1981). Clearly, the birds were neither producer nor scrounger strategists although they could have been alternating between the two at ESS frequencies.

Distinguishing between opportunists and mixed strategists will require a finer-grained analysis of individual behavior. For instance, mixed strategists should be identifiable as individuals that exhibit runs of prey obtained via one strategy and then via the other, a situation comparable to Croze's (1970) description of crows that use searching images. In some situations the existence of opportunists may be quite obvious. Imagine, for example, seabirds exploiting schools of fish. Producer individuals may fly low to increase their probability of detecting a patch when they fly over it. Scroungers may fly high to maximize the number of producers they can observe at a given time. An individual playing a mixed strategy would alternate between flying at the producer height and at the scrounger height. The opportunist strategy, however, would be to fly at an intermediate height that maximizes the chances of detecting others' discoveries while minimizing the reduction in ability of detecting patches. A similar scenario may hold for the frequency of scanning in a ground forager that lowers its head to search but raises it to survey conspecifics. Our model suggests that more attention should be paid to such details of social foraging behavior.

that are capable of influencing the producer's rate of foraging before the arrival of scrounging individuals. Hence, patches that are more diffuse or contain prey items that require long handling times will be depleted more slowly and will offer a larger scroungers' share. Any factor that is likely to influence the rate of arrival of scrounging individuals will also influence the scroungers' share. When scrounging individuals arrive rapidly, the scroungers' share will be larger. Close proximity between individuals or open habitats where others are very visible are likely to promote larger scroungers' shares. The rate of arrival of scrounging individuals may also be affected by group size.

Increasing levels of interference between foragers will likely reduce the scroungers' share but the consequences are not straightforward. For instance, aggression by producers may delay arrival of scrounging individuals and reduce the scroungers' share. If this is so, any factor promoting defensibility of a food source will likely reduce the scroungers' share. If patches of prey become increasingly unavailable on arrival of the producer, the scroungers' share again is likely to decrease (Charnov et al. 1976). Producers can also interfere with other producers (Goss-Custard 1976; Gillis and Kramer 1987; Hake and Ekman 1988). Clearly the effect of interference on the dynamics of foraging in groups of producer and scrounger strategists must be understood better.

When food is found in few localized areas, groups are likely to be larger, favoring a higher relative proportion of scrounging individuals. Similarly, increases in population density may lead to larger groups. Factors that reduce the extent of sensory contact between individuals such as luminosity, turbidity of water, fog, height of undergrowth, wind, and so forth will likely reduce effective group size and thus favor an increased proportion of producers.

Additional Considerations

To simplify the ESS analysis, we have made several simplifying assumptions whose consequences are worth exploring. The main assumptions we deal with here are that all group members are phenotypically similar, strategies are fixed genetically, and all group members are of the same species.

Equal phenotypes.—Our analysis assumes that all individuals are equal. It is very likely, however, that individual phenotypes differ (e.g., in size, age, social rank, c, and h, etc.) and that different strategies are optimal for different phenotypes. In such a case one would need to modify our analysis to include phenotypic limitations. This will most likely influence the expected frequency of each strategy at equilibrium. One possible consequence of individual variation in c and h, for instance, is the coexistence of the three strategies in a wider range of circumstances than predicted by our model. It will therefore be extremely important to determine how much individuals differ and to establish empirically the relationship between phenotype and payoffs obtained from alternative strategies.

Genetic determination of strategies.—The model is based on the assumption that strategies are genetically determined and their frequencies set by frequency-dependent selection. There is some evidence that individual strategies could be fixed in house sparrows (Barnard and Sibly 1981). However, in most circumstances individual strategies appear to be flexible. For instance, in Harris's sparrows, dominants use subordinates as food finders only when food is highly

clumped (Rohwer and Ewald 1981). Similar results have been obtained with dark-eyed juncos (Theimer 1987). In pigeons, scroungers develop into producers when established producers are removed from the flock but revert to scrounging when the former producers are returned (Giraldeau and Lefebvre 1986). There is some evidence that learning can lead to equilibriums that are functionally analogous to ESS (Harley 1981; Maynard Smith 1982; Houston and Sumida 1987). It is possible therefore that the conclusions of our model will pertain to situations in which individuals adjust their behavior in response to their experience. The success of ideal free-distribution models in predicting short-term matching between animal density and food supply indicates that frequency-dependent models can success-fully predict plastic responses (Parker and Sutherland 1986).

Intraspecific systems.—Our model assumes that producers, scroungers, and opportunists share the same gene pool. It has been argued that the ESS analysis applied to intraspecific producing and scrounging can be translated to include interspecific systems (Sibly 1984). Our model will not be easily extended to inter-specific cases because differential food intake will not necessarily be related to differential fitness when more than one species is involved. In systems in which animals adjust their behavior according to payoffs of alternatives, we expect that our model's general predictions will hold even for interspecific systems.

Implications for Sociality

Producer-scrounger models predict that scrounging will be common when prey are worth appropriating and hosts are abundant (Brockmann and Barnard 1979; Barnard 1984). The extent to which these scroungers impose a cost is not entirely clear. In fact, the same producer-scrounger model can apply when scroungers enhance the producers' foraging rate (Parker 1984b). The important characteristics of the producer-scrounger model are that scroungers when rare do better than producers and that the scroungers' payoffs be frequency-dependent. Thus, producer-scrounger models have not dealt extensively with the degree to which scrounging imposes a cost to sociality.

Information-sharing models (Thompson et al. 1974; Pulliam and Millikan 1982; Clark and Mangel 1984) have collapsed the decisions of group membership and scrounging into one. In many cases group membership was shown not to enhance individual foraging rate (Thompson et al. 1974; Pulliam and Millikan 1982). In Clark and Mangel's model, group membership (and thus scrounging behavior) was predicted to spread even when all individuals incurred a loss, a situation they likened to a Prisoner's Dilemma (Axelrod and Hamilton 1981). Our model separates group membership from scrounging decisions. It assumes that individuals are already in a group and asks under what circumstances scrounging behavior will occur. We show that, in any group, even one that has formed for nonforaging reasons, scrounging behavior is very likely to spread and thus decrease every-one's foraging rate. The extent of the social foraging cost depends on the degree of incompatibility between producing and scrounging activities and on the scroungers' share. Group membership, and hence sociality, will often lead to the spread of scrounging behavior. Thus, group foraging, except in the case of coopera-tive hunting (Packer and Ruttan 1988), turns out to be a significant and apparently inevitable cost to sociality rather than a benefit, as it has often been thought.

Since scrounging individuals necessarily impose a cost to producers it is possible that producers would do best by leaving the group to forage either alone or in another group in which scrounging is not present. Solitary foraging may not always be an option, however. In some situations food may be available in localized areas such that the presence of others cannot be escaped. In other situations, predation hazard or other benefits that are provided by the presence of others may be such that it is more profitable to suffer scrounging costs than to forage alone (Baker et al. 1981). The possibility of escaping the presence of others has been explored theoretically by Rubenstein (1978) and empirically by Caraco et al. (1989). This option offers producers some bargaining power in reducing the costs that are imposed by the scrounging individuals. For instance, in situations where scroungers impose high costs, producers may simply leave and forage elsewhere, which thus reduces the benefits to scroungers. There is evidence, for instance, that group-membership decisions of house sparrows are based on the producer-scrounger ratio in the flock (Barnard and Sibly 1981). This could lead to a system of fitness biasing similar to the one described for the evolution of cooperative breeding of anis (Vehrencamp 1984). In the specific situation of social foraging, the extent of scrounging behavior in a group may depend on the profitability of the alternatives available to the producer strategy.

Seeing the spread of scrounging as an inevitable and costly outcome of group membership leads to some interesting predictions. For instance, absence of scrounging within groups may evolve as a result of reciprocal or kin-selected altruism. Thus, small groups of fixed membership or groups of close kin may favor the absence of scrounging. Whereas using the food discovered by others was once thought to be a stepping stone to sociality, it now becomes apparent that refraining from using others' discoveries and thus foraging effectively as solitary individuals would be more likely to provide benefits to group members.

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