

Breeding colonies as information centers: a reappraisal of information-based hypotheses using the producer–scrounger game

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One of the most cited hypotheses for the evolutionary advantages of colonial breeding proposes that colonies serve as a place of information exchange about the location of food—the information center hypothesis. Despite its popularity, the hypothesis generated considerable controversy over its predictions and role in the evolution of colonial breeding. As a consequence, the hypothesis still lingers on, despite numerous apparent falsifications from both observational and experimental approaches. The controversy has three roots: the unclear causal direction between coloniality and information center, the unrecognized distinction between colonial breeding and colonial roosting, and the use of an implicit group selectionist argument. Here we try to clarify this controversy by applying an entirely individual selection-based approach, the producer–scrounger game, to the information center hypothesis. Furthermore, we show how other information-based alternatives of the original information center hypothesis (e.g., local enhancement and recruitment center hypotheses) can be included in a common framework. Our model predicts that individuals relying on information transfer at the colony should be rather common in nature. This prediction is essentially unaltered by the inclusion of either local enhancement or recruitment center. On the other hand, the frequency of leading unknowledgeable individuals (the most accepted sign of information center) is expected to be very low. The model indicates that tests of information-based hypotheses should focus on the expected relative frequency of food-searching flights rather than the frequency of leading. *Key words*: information center, local enhancement, producer–scrounger games, recruitment center. [*Behav Ecol* 12:121–127 (2001)]

The evolution of avian colonial breeding poses somewhat of a paradox. An estimated 13% of living bird species breed in densely packed colonies (Lack, 1968) and do so despite extensive apparent disadvantages to the individual colony members. Colonial breeding may increase ectoparasite infection (Brown and Brown, 1996), increase competition for food, nesting sites, nesting material, and mates, and even lead to kleptogamy (for a review, see Wittenberger and Hunt, 1985). The advantages required to offset such important costs must be numerous and obvious. Yet, to date, little evidence of any strong advantage for colonial nesting has accumulated (Brown and Brown, 1996).

One of the most cited hypotheses for the evolutionary advantages of colonial breeding proposes that colonies serve as a place of information exchange—the information center hypothesis (Ward and Zahavi, 1973). The hypothesis is based on the observation that many colonially breeding birds feed on highly aggregated and abundant food patches whose locations are unpredictable both in space and time (Lack, 1968; Ward and Zahavi 1973; Wittenberger and Hunt, 1985), precisely the conditions that make it onerous to find food (Barta, 1992). Colonies provide the opportunity to reduce these search costs by allowing individuals to obtain information on food location simply by watching the behavior of successful foragers rather than searching for food themselves.

The hypothesis spawned a flurry of tests that generally tend to refute the hypothesis (for a recent review, see Richner and Heeb, 1995). Despite numerous apparent falsifications from both observational and experimental approaches, the hypothesis lingers on, possibly as a result of disagreement over its predictions and role in the evolution of colonial breeding (e.g., Bayer, 1982; Mock et al., 1988; Richner and Heeb, 1995, 1996; Wittenberger and Hunt, 1985; Zahavi, 1996).

The controversy concerning the role of the information center hypothesis in the evolution of avian colonial breeding has three sources. One concerns the causal direction between coloniality and information center, the other an unrecognized distinction between colonial breeding and colonial roosting, and the third the use of an implicit group selectionist argument.

Causal direction

The information center hypothesis (Ward and Zahavi, 1973), as originally presented, claimed that (1) both colonies and roosts serve as places of information transfer about food location, increasing the colony members' individual foraging success (Beauchamp, 1999), and (2) information transfer was the main selective advantage for the evolution of coloniality (Mock et al., 1988; Richner and Heeb, 1995). The problem with this formulation is that support for the first statement does not constitute backing for the second; information transfer could be the consequence of colony formation; colonies could have evolved as a result of advantages that do not concern information transfer (Bayer, 1982; Mock et al., 1988; Richner and Heeb, 1995). In the current study we assume explicitly that the colonies already exist, i.e. we deal with conditions maintaining an information center and not the center's role in the origin of colonial breeding.

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The difference between breeding colonies and communal roosts

The information center hypothesis was formulated to account for both the evolution of colonial breeding and communal roosting. However, there are important differences between the two systems that could have a significant bearing on the formulation of evolutionary arguments. A roosting bird that locates a food patch could benefit by not returning to the roost by saving the travel time and energy needed to commute between the feeding area and the roost and by avoiding parasitism by previously unsuccessful roost mates (Richner and Heeb, 1995). A breeding bird that encounters a food patch, on the other hand, has little choice but to return to its breeding colony regularly if it is to feed its nestlings successfully. So, for a breeding bird the decision is not whether to return to the colony but whether to breed in the colony in the first place. Choosing to breed alone, away from a colony, could avoid the costs of food parasitism resulting from the information center, but not the time and energy costs of commuting between the foraging site and its nest. Consequently, although it is entirely appropriate to ask why a successful forager should return to the colony (the key problem *sensu* Richner and Heeb, 1995) in the case of communal roosts, it is not an appropriate question for colonial breeders (Dugatkin, 1997; Wittenberger, 1981). In the current study we deal specifically with information-based advantages that follow from colonial breeding. For recent treatments of information based advantages of communal roosts, see Mesterton-Gibbons and Dugatkin (1999), Dall (submitted).

Hidden group-selectionist view

In its original formulation, the information center hypothesis does not explain how evolution could favor birds that go out to search for new food patches when following food finders, as a result of information transfer, is more rewarding than searching under the patch distributions hypothesized to promote information centers. The hypothesis overlooks the individual's search cost by emphasizing the collective advantage of the colony as a place of information transfer—a group selectionist view that has led some to abandon the information center completely, replacing it with more realistic evolutionary hypotheses for the origin of colonial breeding (e.g., Buckley, 1997; Richner and Heeb, 1995, 1996; Weatherhead, 1983). Others have failed to recognize that the information center hypothesis must be cast as a game theory problem (e.g., Dugatkin, 1997: 79).

Two information-based alternative hypotheses for colonial breeding

The confusion highlighted above concerning the information center hypothesis has had two important consequences. First, it has prevented the development of quantitative models based on individual selection that could generate widely acceptable and openly testable predictions and hence has hampered our ability to reject the hypothesis more firmly. Second, in the wake of the lack of success of the information center, alternative hypotheses, some harboring the same hidden problems have arisen, confusing the issue even further. We review two of these hypotheses briefly here because as we show, they constitute mere variants of a general information-center hypothesis.

The local enhancement hypothesis (Buckley, 1997; Mock et al., 1988) assumes that birds breed in colonies because colonies increase the local density of foraging birds, which in turn leads to increased probability of patch discovery through cu-

ing on a feeding conspecific's location (local enhancement; Mock et al., 1988; Pöysä, 1992; Thorpe, 1956). In an elegant simulation study, Buckley (1997) showed that the possibility of local enhancement could lead to the evolution of colonial breeding when food distribution is clumped and ephemeral. Showing the effect of local enhancement, however, does not automatically rule out the information center hypothesis as a factor in the evolution of colonial breeding. In the case of Buckley's model, this is especially true because Buckley (1997) did not allow individuals to use the information center.

The recruitment center hypothesis assumes that animals gain from exploiting a patch in groups (Evans, 1982; Richner and Heeb, 1995). Therefore, upon finding a patch an individual gains by recruiting companions to it. The colony then is useful as a means to provide increased certainty that recruits will be found (Richner and Heeb, 1995, 1996). This hypothesis, however, also suffers from a group selectionist view; it does not explain why birds go out to search alone if waiting behind to be a recruit is more profitable.

Toward a unified view of information-based hypotheses for colonial breeding

Breeding colonies provide many documented instances of selfish exploitation of others' efforts: taking of nest materials from unattended nests (Hoogland and Sherman, 1976), extrapair copulations (Møller and Birkhead, 1993), intraspecific brood parasitism (Brown and Brown, 1996), and food kleptoparasitism (Wittenberger and Hunt, 1985). The exploitation of food-finding efforts, therefore appears a reasonable expectation, and so we apply a game-theoretic model of selfish exploitation to the problem of information transfer at the breeding colony, recognizing that the process of information exchange likely corresponds to a producer–scrounger game (Barnard and Sibly, 1981; Giraldeau, 1997).

The producer–scrounger game was first proposed to investigate the exploitation of others' food-finding efforts in foraging flocks (Barnard and Sibly, 1981). The model assumes that individuals can use two alternative foraging tactics: producer and scrounger. Producer is a tactic that actively searches for new food patches. Scrounger waits (or searches) for successful producers and moves in to exploit the food (Barnard and Sibly, 1981; Giraldeau and Beauchamp, 1999). The game assumes that the scrounger tactic does better than the producer tactic when few individuals use scrounger because abundant exploitable food patches are made available by the many individuals playing the producer tactic. The scrounger tactic does worse than the producer tactic when it is common. The reason is twofold: first, many fewer food patches are available as a result of the lower number of individuals engaged in playing producer, and second, the number of individuals competing within the scrounger tactic is larger. This strong negative frequency dependence of payoffs leads to a mixed evolutionarily stable strategy (ESS; Maynard Smith 1982), where both tactics obtain equal pay-offs if players are phenotypically equal. Formal theoretical models have shown that the evolutionarily stable proportion of scrounger in foraging groups depends on (1) the proportion of a food patch consumed by the producer individual before the arrival of the scroungers, the finder's share (Caraco and Giraldeau, 1991; Vickery et al., 1991); (2) the dominance structure of the flocks (Barta and Giraldeau, 1998); and (3) the energy reserves of the foragers (Barta and Giraldeau, 2000; Caraco and Giraldeau, 1991). Some empirical results support the models' predictions (see Giraldeau and Beauchamp, 1999, for a review).

An information center can function as a producer–scrounger game. Assume that a bird finds food patches according to a Poisson process with rate λ . Under this assumption the av-

Table 1
Conditions for producer–scrounger games (after Caraco and Giraldeau, 1991) and how the information center game fulfils them

Producer–scrounger game	Information center game
Two exclusive strategies: Producer uncovers new resources Scrounger exploits producer's efforts	Two exclusive strategies: Searcher discovers new food patches Wait-and-follow exploits searcher's food finding efforts
Scrounger has high payoff when scrounger is rare	Wait-and-follow strategist could follow many searchers when wait-and-follow tactic is rare
Scrounger's payoff is strongly and negatively frequency dependent	If no one searches, none can be followed

erage time needed to find a patch is $1/\lambda$ (Clark and Mangel, 1986). If N_S birds look for food independently and each finds patches with rate λ then the average time needed to find at least one patch by them is $1/(\lambda N_S)$, which is much less than $1/\lambda$ (assuming $N_S > 1$) (Clark and Mangel, 1986). Therefore, a bird that is able to detect its companions' food patches will exploit patches more often. For a colonial breeder, one possible way to locate others' food patches is to wait at the colony and follow successful returnees on their next trips to their previously discovered foraging patch—that is, use the colony as an information center. This wait-and-follow tactic, much like scrounger, prospers for two reasons: it can locate food patches more frequently than birds searching themselves, and it saves the time and energy spent on searching. Therefore, the wait-and-follow strategy can spread in the colony, so long as the patch has enough food after it is discovered and it exists long enough to allow its finder to return at least once. Of course, as is true of scrounger, the wait-and-follow tactic cannot be stable alone; if no one goes out to find novel food locations, then none will be available to be exploited. This is precisely why the producer–scrounger game theoretical approach is appropriate for all three information-based hypotheses (Table 1).

The information center as a producer–scrounger game

We assume that birds breed in a colony of size N . The individuals feed, by returning n times, on ephemeral food patches that disappear before birds can completely exploit them. As a consequence, n is independent of the number of birds foraging on the same patch (i.e., no competition for food). On each trip the birds consume a meal of A and then depart to feed their nestlings. A round trip between the patch and the nest, including the time needed to consume a meal and to feed the nestlings, requires t time units. After the disappearance of a known food patch, the individuals can choose between two exclusive food-finding tactics—search or wait-and-follow. Searchers start a new food-finding trip without returning to the colony (“peripheral switching” sensu Waltz, 1982). They find food patches as a Poisson process with rate λ . Let the time needed for a round trip be equivalent to one time unit (i.e., $t = 1$) so that λ gives the number of food patches found during the time of a round trip. We assume quite reasonably that finding a patch takes longer than the commute between it and the nest, so that $\lambda < 1$ in all cases. Individuals using wait-and-follow, in contrast, return to the colony and wait there for a bird returning successfully (i.e., with food) and follow it on its next foraging trip to its previously discovered foraging patch (“central place switching” sensu Waltz,

1982). Note that both searchers and wait-and-follow individuals can lead others to the food patch, but searchers always return successfully (i.e., with food) according to our definition, while wait-and-follow individuals can be both successful or unsuccessful returnees, and only wait-and-follow individuals can follow leaders.

Under the above assumptions, the food intake rate for an individual playing searcher is

$$R_s = \frac{nA}{n + (1/\lambda)}, \quad (1)$$

and for a wait-and-follow strategist it is

$$R_f = \frac{(n - 1)A}{n + (1/\lambda Np)}. \quad (2)$$

Wait-and-follow strategists take $n - 1$ meals from a patch because they reach it only when the discovering searcher has already taken a meal from it. They take n foraging trips to the patch because they return to the colony instead of starting a new search when the patch disappeared. The proportion of searchers in the colony is p , and λNp gives their combined food finding rate (Clark and Mangel, 1986). This is based on the assumption that wait-and-follow strategists get to know all of the patch discoveries of searchers. The searchers' gains do not depend on their proportion, while the gains of wait-and-follow strategists decline steadily with increasing proportions of that strategy ($1 - p$; i.e., it is negatively frequency dependent). It can be shown that the information center game as outlined here fulfils all of the conditions of the producer–scrounger game (Table 1).

At equilibrium, if all players have equal phenotypes, both searchers and wait-and-follow strategists should have the same food intake rate (Caraco and Giraldeau, 1991; Maynard Smith, 1982; Vickery et al., 1991). This gives the equilibrium proportion of searchers as

$$\hat{p} = \frac{1}{N(1 - \lambda - 1/n)}. \quad (3)$$

As Equation 3 reveals, wait-and-follow strategy cannot be a pure strategy, and so searchers are never totally eliminated from the colony. This provides an evolutionary answer to the key question of why any bird should search when it pays more simply to wait and follow. The information center game does not require any other a priori group foraging benefit to keep the searchers searching and recruiting.

According to Equation 3, the wait-and-follow strategy can spread in the population (i.e., $\hat{p} < 1$) if $\lambda < 1 - 1/N - 1/n$; that is, if it is difficult to find new patches (i.e., large searching cost can be saved), the colony is large (many opportunities to follow someone), and the patches can be visited several times (it is worth returning to a discovered patch). This prediction concurs with previous considerations (e.g., Allchin, 1992; Barta and Szép, 1992, 1995; Erwin, 1977; Waltz, 1982).

Comparing the energy intake of searchers (Equation 1) and wait-and-follow strategists (Equation 2) in a colony of N_S searcher and one wait-and-follow strategist (i.e., $N = N_S + 1$) reveals that an individual should always join a colony of N_S searchers and play as a wait-and-follow strategist if $1 - 1/N_S > \lambda + 1/n$. This means that an originally small aggregation of only a few searchers (as few as two) will grow quickly into a much larger colony containing mostly wait-and-follow strategists so long as the foraging patches can be visited several times (i.e., $n > 2$) and they are hard to find (i.e., $\lambda < 1/6$ for $n = 3$). Another prediction of this model is that the number of searchers in breeding colonies should always be kept very low (as low as two, independently of colony size) given

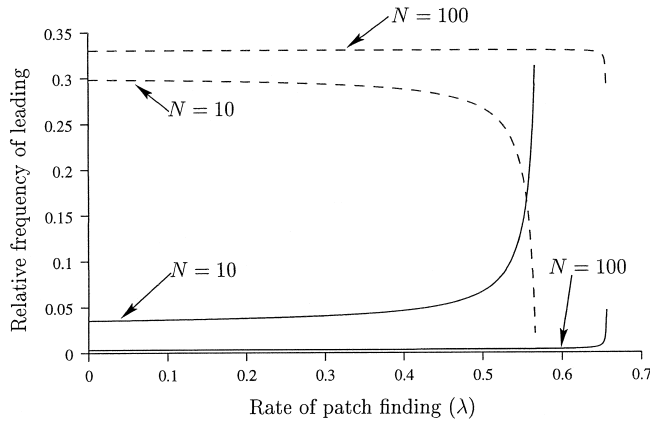


Figure 1
The proportion of leadings (i.e., departure flights on which a bird is followed by others to all departures) as the function of patch finding rate (λ) at different colony size (N). Proportion of leadings can be used to estimate the observable frequency of information transfer at the colony. Because the accurate proportions depend on the details of the information transfer process (see text), the information center game can only provide maximum (dashed lines) and minimum (solid lines) estimates ($n = 3$ for all cases).

that conditions for the growth of the originally small aggregation continue to hold.

Let us express the frequency of information transfer as the proportion of departures involving leading wait-and-follow strategists to all departures from the colony during time T . During T time units, \hat{N}_s searchers find $\hat{N}_s\lambda T$ food patches. Information about the location of these patches is passed on to the $N - \hat{N}_s$ wait-and-follow strategists. The searcher and the wait-and-follow strategists exploit a patch for $n(1 + N - \hat{N}_s)$ departures. Therefore $\hat{N}_s\lambda T n(1 + N - \hat{N}_s)$ departures occur during T . From these departures leadings can occur either $\hat{N}_s\lambda T$ times when the food discoverer leads all wait-and-follow strategists to the patch on a single departure, or $\hat{N}_s\lambda T(N - \hat{N}_s)$ times when all wait-and-follow strategists are led to the patch one at a time (note that individuals playing the wait-and-follow tactic can also act as leaders). Any other frequency between these minimum and maximum estimates, depending on the details of the information transfer process, is possible. It follows, after some calculus, from the above that the minimum proportion of information transfer to all departures is

$$\frac{1}{n\left(1 + N - \frac{1}{1 - \lambda - 1/n}\right)}, \quad (4)$$

whereas the maximum proportion is

$$\frac{N - \frac{1}{1 - \lambda - 1/n}}{n\left(1 + N - \frac{1}{1 - \lambda - 1/n}\right)}. \quad (5)$$

Examination of these estimates (Figure 1), however, reveals that they are not very useful predictors of the frequency of information transfer because they go to different limits as N increases and λ decreases. These equations predict, however, that the frequency of information transfer can be low in a colony of individuals playing the information center game.

A more useful sign of the operation of an information center can be derived if one can distinguish food-searching flights from transit flights directed to known patches. The distinction

between these two types of flights could perhaps be based on the analysis of the whole flight path. One can expect that individuals going to a patch of known location fly to it using a less circuitous route than individuals who encounter a patch after having searched for it. It is also possible that transit and search flights are characterized by distinct altitudes. If transit and search flight types can be distinguished, then our game makes a unique prediction that could help experimentalists test the information-center hypothesis more effectively. The searchers find $\hat{N}_s\lambda T$ food patches on the same number of food-searching flights. These patches are exploited by $\hat{N}_s\lambda T n(1 + N - \hat{N}_s)$ departures, all of which except $\hat{N}_s\lambda T$ are transit flights to known patches, either because individuals know the location of the patches or because they are led to them. It follows that the proportion of food-searching flights to all flights is

$$\frac{1}{n\left(1 + N - \frac{1}{1 - \lambda - 1/n}\right)}. \quad (6)$$

This proportion goes to zero quickly with increasing N and n as well as with decreasing λ , implying that one can expect to detect food searching flights only very rarely if the information center operates, especially in large colonies feeding on rare patches visitable several times. Increasing N and decreasing λ reduces the proportion of searchers and so decreases the proportion of search flights. Raising n , in contrast, increases the number of visits to a discovered patch, which naturally also leads to decreasing proportion of search flights. Comparing Equation 4 to Equation 6 reveals that the frequency of food-searching flights never exceeds the frequency of departures involving the leading of wait-and-follow strategists (i.e., the frequency of information transfer at the colony).

Local enhancement and recruitment center hypotheses as variants of the producer–scrounger information center game

In the following sections we show how the local enhancement and recruitment center hypotheses for the evolution of colonial breeding can be included in the information center game and how predictions of the information center hypothesis are changed by doing this. First we consider the local enhancement hypothesis. We keep all of the assumptions of the information center game but add one—namely, that searchers can also be informed of the food discoveries of other searchers. This increases the searchers’ foraging rate from λ to $\lambda + \lambda a(Np - 1)$ (given $Np > 1$), where $0 \leq a \leq 1$ is the efficiency of the local enhancement (LE). If $a = 0$ there is no local enhancement while $a = 1$ means that a searcher gets information about all of the food patches discovered by the other $Np - 1$ searchers. While the food-finding rate of individual searchers increases, we also assume that their combined corporate feeding rate does not change; the patch exploitation time is negligible compared to search time. So all searchers look for food during almost all the available foraging time. Based on this assumption, the food intake rate for a searcher using local enhancement (given $Np_{LE} > 1$) is

$$R_{S,LE} = \frac{nA}{n + \frac{1}{\lambda[1 + a(Np_{LE} - 1)]}}, \quad (7)$$

whereas that of a wait-and-follow strategist is

$$R_{F,LE} = \frac{(n - 1)A}{n + \frac{1}{\lambda Np_{LE}}}. \quad (8)$$

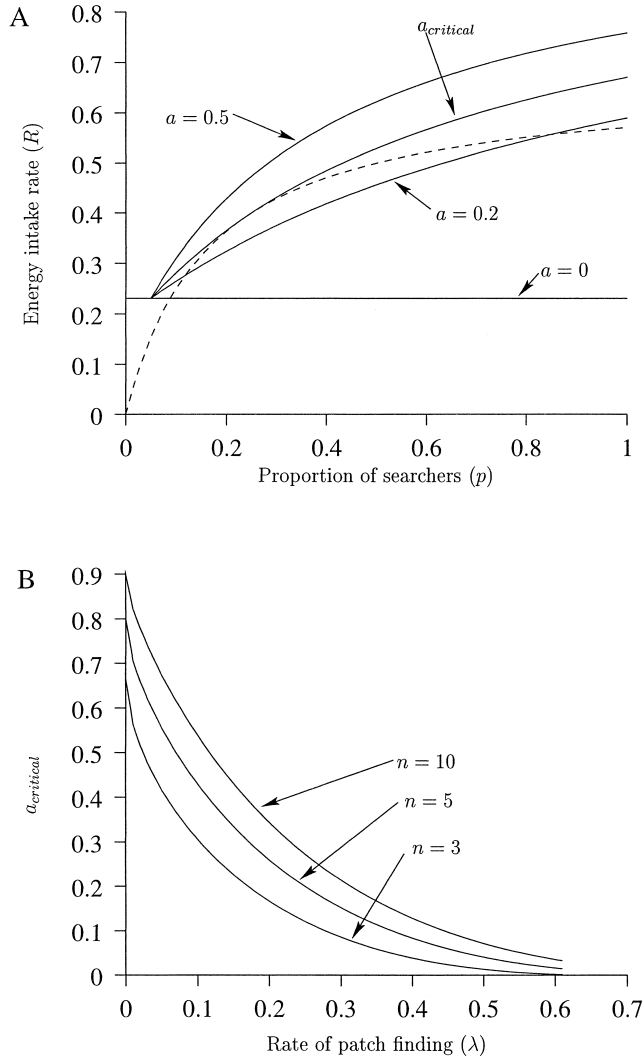


Figure 2
 (A) The energy intake rate of wait-and-follow strategists (dashed line) and those of searchers (solid lines) drawn against the proportion of searchers in the colony under different efficiency of local enhancement (a). The intersection of dashed and solid lines marks the equilibrium proportion of searchers (\hat{p}) when the payoffs for the two strategies are equal. When a solid line crosses the dashed line twice (e.g., $a = 0.2$), only the smaller \hat{p} is stable. The colony is driven from the equilibrium point marked by the higher \hat{p} by small deviation from it either to the stable (lower) equilibrium point or to the fixation of searchers depending on the sign of the bifurcation. $a_{critical}$ marks the critical level of local enhancement above which no wait-and-follow strategists can exist in the colony because the energy intake rate for searcher is higher for all values of p ($N = 20$ for all cases). (B) The effect of patch finding rate (λ) and number of patch visits (n) on the critical level of local enhancement ($a_{critical}$).

The equilibrium proportion of searchers in this local enhancement scenario, \hat{p}_{LE} , by making Equations 7 and 8 equal, can be calculated by solving the following equation

$$a\lambda N^2 \hat{p}_{LE}^2 + \left[(1-a)(\lambda-1) + \frac{1}{n} \right] N \hat{p}_{LE} + (1-a) = 0. \quad (9)$$

This equation has two roots from which only the smaller one gives a stable proportion of searchers (for explanation see Figure 2a). Comparing Equation 9 to a similar construct for the no local enhancement scenario (Appendix) reveals that

the stable proportion of searchers under the local enhancement scenario, \hat{p}_{LE} , is always greater than the equilibrium proportion of searchers without local enhancement, \hat{p} , given that $a > 0$. Making the determinant of Equation 9 equal to zero and solving this equation for a gives the critical value of a above which no wait-and-follow strategist can persist in the colony (Figure 2a).

$$a_{crit} = \left[1 - \frac{1-\lambda}{n(1+\lambda)} - \sqrt{\left(\lambda + \frac{1}{n} - \frac{1-\lambda}{n(1+\lambda)} \right) \left(2 - \lambda - \frac{1}{n} - \frac{1-\lambda}{n(1+\lambda)} \right)} \right] \div (1+\lambda). \quad (10)$$

From Equation 10 it can be seen that local enhancement should be effective in preventing wait-and-follow strategists from spreading (Figure 2b) when it is hard to find food (low λ) and patches can be visited several times ($n > 2$)—precisely the conditions under which one can expect the spread of wait-and-follow strategists (see above). This very effective local enhancement, however, can be an unreasonable assumption because most colonial species search for food in a vast space, making it unlikely that a searcher would ever get to know about all others' food discoveries (consider, for instance, the case when they are searching in opposite directions from the colony). Therefore, one may expect to encounter wait-and-follow strategists in almost every colony despite local enhancement.

One can model the recruitment center (RC) hypothesis (Richner and Heeb, 1995, 1996) keeping the same assumptions as the information center game by allowing meal size (A) to be larger when the wait-and-follow strategists reach the patch (the group foraging advantage). Note that we do not consider here the case of active recruitment—that is, successful patch finders do not advertise their findings actively. The often complex displays that are assumed to be signs of active recruitment (Richner and Heeb, 1996) may not be as relevant for colonies as they are for communal roosts. Under these conditions the food intake rate for a searcher in the recruitment center is

$$R_{s,RC} = \frac{A + (n-1)bA}{n + 1/\lambda}, \quad (11)$$

where $b > 1$ marks the benefits of group foraging (see Richner and Heeb, 1995, 1996, for possible mechanisms). In a recruitment center the wait-and-follow strategist's gain is

$$R_{f,RC} = \frac{(n-1)bA}{n + \frac{1}{\lambda N p_{RC}}}. \quad (12)$$

Equating Equations 11 and 12, one gets the equilibrium proportion of searchers to be

$$\hat{p}_{RC} = \frac{1}{N} \frac{1 + b(n-1)}{b(n-1) - \lambda n}. \quad (13)$$

This proportion of searchers is always smaller than the proportion of searchers without recruiting, \hat{p} , (given $b > 1$), that is, wait-and-follow strategists spread more in recruitment centers than they do in information centers. This prediction holds when the group foraging benefits can depend on the group size so long as these benefits are non-zero.

DISCUSSION

In this article we clarified three sources of confusion concerning the information center hypothesis that have also affected

to some extent two alternative information-based hypotheses. We proposed a cogent answer to the key question of why any individuals actively search for food when following food finders is hypothesized to be more beneficial. We modeled the information center as a producer–scrounger game with specific tactics of search and wait-and-follow. By doing so we provided an entirely individual selection-based interpretation for the operation of information centers. The game shows how the benefits of a wait-and-follow strategy can be negatively frequency dependent. As a consequence, the game predicts a mixed ESS solution where searchers are never completely excluded from the breeding colony. This means that, even in the absence of any mutual benefits, there will always be individuals who leave the colony to find new food patches and hence provide exploitation opportunities to other colony members. Basically, searchers are kept by virtue of the extra meal they obtain from the discovered patch—an advantage that is similar to the finder's share in foraging flocks (Caraco and Giraldeau, 1991; Vickery et al., 1991).

It is important that the model does not require individuals to specialize in a given role and either search or wait and follow exclusively. What is required is that the proportion of strategies be kept at the equilibrium value. Individuals can achieve this either by specializing or by randomly alternating between strategies or by any mixture in the population that yields the stable proportion (Giraldeau and Livoreil, 1998).

The detailed investigation of the equilibrium proportion of searchers shows that only a few individuals should leave the colony to search for novel locations of food. As a consequence, a large part of the colony is expected to be playing wait-and-follow and rely on the patch location information provided by the returning searchers. This picture is not significantly modified by allowing local enhancement (Buckley, 1997; Thorpe, 1956) or recruitment centers (Evans, 1982; Richner and Heeb, 1995) to operate. In fact, our analysis reveals that the recruitment center increases the proportion of colony members relying on information transfer at the colony beyond expectations of the simpler information center hypothesis. It is true that local enhancement can lead to the elimination of the wait-and-follow strategy but does so only if local enhancement is extremely, and perhaps unreasonably, efficient, allowing all birds to monitor the success of all others concurrently. At moderate efficiencies of information transfer by local enhancement the equilibrium proportion of searchers is affected only negligibly. As a consequence, one may expect information transfer on food location at the colony to be rather common in nature, independently of whether local enhancement or recruitment center mechanisms operate.

Predicting that information centers should be common may appear paradoxical given that only a small number of published studies clearly support the operation of information centers at breeding colonies (Brown, 1986; Greene, 1987; but see Fleming, 1990; Gori, 1988; Waltz, 1987). This paucity of support is especially daunting given the considerable research effort invested in testing the hypothesis (for a review, see Richner and Heeb, 1995). Our game theoretic model, however, suggests that the empirical basis used to reject the occurrence of information centers may not have been entirely appropriate. Our model predicts, for instance, that frequent cases of leading (the most commonly assumed sign of the operation of an information center) should only be expected when the colony members exploit extremely ephemeral food patches where n is very close to 2. Therefore, it may not be so surprising that one of the few instances of support for the information center based on such evidence comes from a study of cliff swallows (Brown, 1986) that fed on highly ephemeral food patches that usually existed no longer than 20–30 min (Brown and Brown, 1996). Our model also pre-

dicts that information transfer events can be rare, and therefore difficult to observe, if individuals can visit a patch several times. The consequences of the possibility of low frequency of leading are twofold. First, this may explain why only a handful of studies support the operation of information centers. Second, the information center game still cannot be convincingly falsified simply by documenting the absence of leading. Our game theoretic model, however, offers an alternative means to falsify the information center hypothesis.

The information center game predicts that the proportion of food searching flights to all departures should never exceed the proportion of leading when the information center is at work. One way to get such evidence would be to use remote-sensing techniques to trace the whole flight paths of individuals leaving the colony (e.g., Benevenuti et al., 1998; Kenward, 1987; Priede and Swift, 1994). One could convincingly reject the information center hypothesis by showing that the frequency of food-searching flights from the colony exceeds the frequency of information transfer as measured by instances of leading.

Both local enhancement and recruitment center hypotheses are consistent with an increased foraging efficiency and so may be more promising candidate hypotheses for the evolutionary origin of avian colonial breeding (Beauchamp, 1999). Because the gain obtained by the searcher strategy does not depend on its frequency and the two strategies' gains are expected to be equal at equilibrium, the information center hypothesis is not consistent with an increase in the foraging efficiency of colonial individuals. As a consequence, its role in the origin of colonial breeding can be questionable. But if more than two searchers aggregate initially, for whatever reason, it would always be profitable for subsequent individuals to join them to play the wait-and-follow strategy rather than to attempt breeding alone. So even if the information center is not involved in the original aggregation of the first two individuals, it could play a role in inflating the initially small aggregation into a large breeding colony. Thus the information center cannot be ruled out completely as a factor in the evolution of breeding colonies. An individual-based simulation to investigate this aspect of information center is under way.

APPENDIX

The solution of the following equation gives the equilibrium proportion of searchers in baseline condition:

$$pN\left(\lambda - 1 + \frac{1}{n}\right) + 1 = 0. \quad (\text{A1})$$

Solving the following equation gives the stable proportion of searchers under the local enhancement scenario:

$$a\lambda N^2 p_{LE}^2 + N\left\{(1 - a)(\lambda - 1) + \frac{1}{n}\right\}p_{LE} + 1 - a = 0. \quad (\text{A2})$$

After reordering this equation becomes:

$$p_{LE}N\left(\lambda - 1 + \frac{1}{n}\right) + 1 + a\lambda N^2 p_{LE}^2 - a(\lambda - 1)Np_{LE} - a = 0. \quad (\text{A3})$$

Subtracting Equation A1 from A3 gives the difference between the stable proportion under the different scenarios:

$$p_{LE} - p = Npa\left[\lambda Np_{LE}^2 + (1 - \lambda)p_{LE} - \frac{1}{N}\right]. \quad (\text{A4})$$

Because the formula in the bracket is always larger than zero, the stable proportion of searchers under the local enhance-

ment scenario is also larger than under the baseline condition, given $a > 0$.

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