Is the Information Center Hypothesis a Flop?

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I. INTRODUCTION

The sight of some thousands of crows chattering and fighting at sunset in the canopy of a small wood is spectacular, and evokes our feelings of the fun and complexity that surround social life. Birds arrive there from their daily feeding sites many miles away. and return to them the next morning, or perhaps go somewhere else. We are impressed by the view of a breeding colony of tens of thousands of gannets, stuck to a small rock in the North Sea, commuting over long distances to find food for their hungry chicks. Likewise. communal roosting or breeding is typical for many species of birds, mammals. and insects.

Two decades ago, in a stimulating paper, Ward and Zahavi (1973) reached the provocative conclusion that "communal roosts, breeding colonies and certain other bird assemblages have been evolved primarily for the efficient exploitation of unevenly-distributed food sources by serving as information centres." This has become known as the information center hypothesis. As one can see, the provocation is double, as it is first implied that roosting in birds serves to gather information about location of food, and second, that the benefits arising from this information transfer have been the driving evolutionary force that led to communal roosting or breeding. The general view at the time was that the function of communal roosting or breeding is rather found in an efficient protection from predators (e.g., Lack, 1968). Ward and Zahavi's proposition has been fruitful in generating many studies attempting to test the hypothesis, and their paper became the citation classic of the journal in which it was published.

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A. HISTORY OF THE HYPOTHESIS

Fisher (1954) first proposed the idea that group living in birds may be beneficial for feeding. He reviewed the literature back to the study of the griffon vulture (*Gyps fulvus*) by Tristram (1859), who wrote:

> The Griffon who first descries his quarry descends from his elevation at once. Another, sweeping the horizon at a still greater distance, observes his neighbour's movements and follows his course. A third, still further removed, follows the flight of the second; he is traced by another; and so a perpetual succession is kept up so long as a morsel of flesh remains over which to consort.

Fisher (1954) summarizes his own observations on feeding fulmars as follows:

> some very mobile species of seabirds, such as fulmars, often give the impression of being individually dispersed when in fact the individuals are all part of a "stretched flock"—a great network of beaters spread to the limit of practical neighbour watching, so that the discovery of one can become the prey of all the hunters of a wide sea area,

concluding

> that a flock can detect and exploit a swarm more efficiently and thoroughly than individuals.

Both Tristram's and Fisher's observations support the simplest concept of a food-related grouping behavior, called "local enhancement" (Hinde and Fisher, 1951; Fisher, 1952). The understanding of this concept has some relevance here, since the findings of many studies claiming evidence in favor of the information center hypothesis are better explained by this more parsimonious mechanism. Thorpe (1956) defined local enhancement as "an apparent imitation resulting from directing an animal's attention to a particular part of the environment," and Mock, Lamey, and Thompson (1988) refer to local enhancement as "cueing on other already foraging birds for food information." The widest definition is given by Galef (1988) as "a tendency on the part of naive individuals to approach conspecifics, alterations conspecifics have made in the environment, or objects they have contacted."

Ward (1965) first contrasted the idea of local enhancement with his new hypothesis (to which he did not attach a name at the time):

> "local enhancement" . . . is practicable only over a limited area within which birds can see each other. It seems likely that the main function of the roost is to extend the benefits of this kind of feeding, so that social feeding may be practiced by a population

together exploiting an area of hundreds of square kilometers. It seems reasonable to suppose that when the members of a roost fly out at dawn, their behaviour will depend partly on their success during the previous day. Those individuals which have left a good feeding place the evening before probably return to the same area, while those that have been less fortunate do not. It would obviously benefit the latter if, instead of going on a random search of new feeding grounds, they could simply join a group whose behaviour indicated that they were heading for an area where food was to be had.

Horn (1968) observed that nestling Brewer's blackbirds (*Euphagus cyanocephalus*) in the center of a colony gained more weight per day than young of the same age in peripheral nests, and suggested that this is so because central birds have more neighbors from which they could learn the location of food patches. In support, he described three cases of birds following successful foragers to new food sources.

Zahavi (1971) later proposed that the predator avoidance function of bird roosts and breeding colonies is of minor importance compared to the foraging advantage through the mechanism proposed by Ward (1965), for which Zahavi coined the term *information center*. If anything, the spectacular aerial displays at the roost or at preroost gatherings as are typical for many species (e.g., swallows, *Hirundo rustica;* bee-eaters, *Merops superciliosus;* starlings, *Sturnus vulgaris;* pink-footed geese, *Anser brachyrhynchus*) may not only advertise the roost to conspecifics, but also to predators (Zahavi, 1971). Zahavi recognizes the existence of adaptations against predation in the communal roost, but clearly views these antipredator adaptations as a consequence of the increase in predation pressure at roosts. The antipredator behavior seen in many roosting species should therefore not be interpreted as a proof of the hypothesis that roosts evolved to minimize predation. Ward and Zahavi (1973), in a major review, concluded enthusiastically that the evidence from many studies clearly favors the information center hypothesis, and that even the exceptions (e.g., solitary feeders with communal roosts, or flock feeders roosting solitarily) could be explained by the same mechanism. Somewhat disenchanting was the extensive review of the evidence for the information center hypothesis by Mock *et al.* (1988): of the many studies covering the fifteen years between the two reviews, only a few provided support for the hypothesis that individuals at roosts or colonies exchange information about location of food patches. In particular, local enhancement (Ward, 1965; Hinde, 1961; Thorpe, 1956) could often not be excluded.

The most important difference between the concept of local enhancement and the concept of an information center concerns the location of information transfer between individuals: local enhancement occurs at the food patch and the increase of group size arises as a consequence of

birds cuing on already foraging animals. An information center is localized away from the food patch and supposedly arises as a consequence of animals seeking information from successful foragers about the location of the distant food source. The information center mechanism requires communal nesting or roosting, whereas local enhancement does not. We do not discuss here the several hypotheses of colonial behavior based on local enhancement (e.g., Morrison and Caccamise, 1985; Caccamise and Morrison, 1986).

B.   SOME CONDITIONS UNDERLYING THE INFORMATION CENTER MECHANISM

The many papers that have investigated the information center hypothesis often assume implicitly or explicitly that a number of conditions must be fulfilled for a roost or breeding colony to function as a center where unsuccessful foragers can obtain information for food finding. In particular, if a test of the information center hypothesis provides negative results, it cannot be used as evidence against the hypothesis unless it was shown that these conditions were fulfilled.

For simplicity, and unless otherwise specified, we will from now on refer to both a breeding colony and a communal roost as a colony. The following are the necessary conditions:

1. The food is patchily distributed in space and/or shows ephemeral occurrence in time. This creates a need for information about its location and time of occurrence. A larger number of birds will then have a higher chance to detect a food source.

2. Food patches are rich in order to reduce competition within the patch.

3. The duration of a food patch allows at least one return trip to the colony and back to the patch.

4. Successful foragers return to the colony after having located and exploited a food patch.

5. The colony members can distinguish between successful and unsuccessful foragers. The discrimination is possible on the basis of the feeding success achieved on the immediately preceding foraging trip.

6. After a visit to the colony, the successful foragers return to the previously discovered feeding site.

7. Differences in foraging success between individuals arise by chance

in the localization of food or by differing abilities to localize food, not as a consequence of competitive ability or differences in exploitation rates.

8. Unsuccessful foragers that follow others are more successful on their next feeding excursion than unsuccessful foragers that do not follow.

Most of these conditions are obvious, but little is usually said about the circumstances that make them likely to be fulfilled. We attempt to provide insight (Section II) into the circumstances that make it more likely that some conditions may be met, and will also analyze a few predictions (Section IV) that pertain to some of the above conditions.

C. The Key Problem

The key problem for the functioning of colonies as information centers concerns the question of why a successful forager should return to the colony and thereby have to pay the time and energy cost of the trip from the food patch to the colony and back, and furthermore suffer from the costs of being followed by parasitic, previously unsuccessful foragers. Ward and Zahavi did not explicitly address this problem. Mock *et al.* (1988) have proposed a graphic model of the cost-benefit balance of leaders and followers that distinguishes between parasitic and mutualistic relationships (Fig. 1). They state that "an information center mechanism can evolve only when the Follower (f-axis) benefits and the Leader (l-axis) does not suffer a great net cost relative to the Follower's net gain. The shaded area shows this set of conflicting interests."
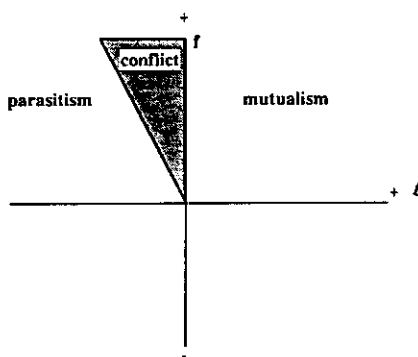

FIG. 1. Model showing the zone of conflicting interests of leaders and followers for which the information center mechanism has been proposed. Adapted from Mock et al. (1988).

The problems with this interpretation are the following:

First, without further assumptions of cooperation or kin benefits, the shaded area is not a zone of conflicting interests, since it is no advantage to the successful forager to suffer a cost, even if the unsuccessful forager gets a relatively higher benefit than the costs it presents to the successful one. Therefore the returning successful forager suffers a reduction in energy intake arising from being followed to the patch and, for example, having to share the food. This energetic cost (L_1) per se raises the question of why a successful forager should return to the colony. Section II illustrates some of the factors that increase or reduce the magnitude of group size-related foraging cost, or factors that can even make group foraging beneficial (i.e., where individuals can derive mutual benefits).

Second, even if the costs to the successful forager of being followed are small or absent, the question remains of why the successful forager should pay the cost of spending time and calories (i.e., L_2 in terms of net energy costs) to return to a colony and back to the food patch. A nonreturning individual would at least save these costs of the return flight and, in terms of fitness, do better than a returning one.

The information center mechanism, as originally proposed by Ward and Zahavi, rests on the assumption that the individuals participating in an information center benefit and lose in turn, and by chance. The information center hypothesis therefore assumes that the altruistic act of an individual is reciprocated by others in the future.
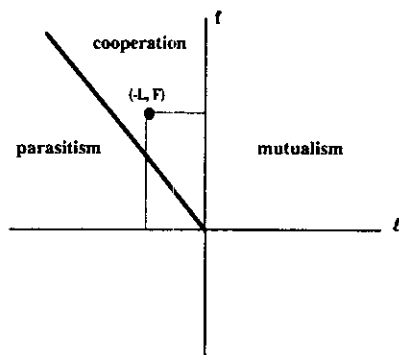

FIG. 2. Conditions where reciprocal cooperation is expected to evolve. Returning to the colony is beneficial to both leaders and followers under the conditions (1) that they strictly alternate roles, and (2) that the costs to the leader are smaller than the benefits to the follower, that is, the slope of the solid line is steeper than -1.

Reciprocal cooperation is beneficial if the benefits (F) to the receiver of the cooperative act are higher than the costs (L) to the actor (Trivers, 1971; see Fig. 2 for an example. L is composed of $L_1 + L_2$, as explained above). Slopes of the line depicted in Fig. 2 steeper than -1 will therefore satisfy the condition $F > -L$. Therefore, reciprocal cooperation is necessary if the successful foragers are expected to return to a colony. However, theory rather predicts defection as the best strategy for the cases where defection has a high initial payoff (e.g., free riders in large groups), or if cheaters cannot be identified, or also for highly mobile animals (Enquist and Leimar, 1993). Without reciprocated cooperation, the originally proposed information center mechanism rests on group selection. This view is discussed further in Section III. The need for cooperation renders the information center hypothesis, as initially proposed, even more unlikely as an explanation for the evolution of coloniality. Models that are not based on the need for cooperation are also presented in Section III.

D.   INFORMATION TRANSFER AND THE EVOLUTION OF COLONIALITY

As pointed out above, the information center hypothesis claims, first, that information about location of food patches passes from successful to unsuccessful foragers at the communal site, and, second, that this information transfer was the main selective force for the evolution of coloniality. It is important to realize that (1) the observation of information transfer at the colony does not prove the information center hypothesis because several other models also predict information transfer at the colony, and (2) the observation of information transfer does not prove that selection for colonial behavior is acting. These points are illustrated in Section III.

Of the many studies that have been undertaken, most have failed to provide unequivocal evidence for the process of information transfer, as documented in the review by Mock *et al.* (1988) and by others (e.g., Wittenberger and Hunt, 1985; Weatherhead, 1987; Richner and Marclay, 1991). Several predictions of the information center hypothesis will be analyzed in the light of more recent theories in Section IV. The relevant literature concerned with the information transfer is reviewed in Section V.

II.   COLONY-BASED GROUP FORAGING

If animals use roosts and colonies as a center to obtain information about the location of food, this will necessarily lead to an increase of

group size at the food patch. This in turn will lead to increasing competition for food. The costs of group size in colony-based foraging are, however, reduced if food patches are rich and ephemeral. For a further understanding of the information center hypothesis and its alternatives, it is useful here to consider the relationship between individual feeding rate and foraging group size, and explore from a theoretical point of view the effects of group size on the mean and variance of the feeding rate, on risk sensitivity and on an individual's decision to join a colony, and the effect of other factors in promoting coloniality. The aim of Section II is not to review the extensive literature on these topics, but rather to provide a conceptual frame that will highlight the complexity involved in the evolution of information transfer and coloniality.

Does group size affect an individual's feeding rate? Let $F(n)$ be the feeding rate of an individual as a function of group size n, A is the amount of food available to the foragers in a patch, B is the patch exploitation time for one individual, and C is the number of patches discovered in a given time. Thus $1/C$ is the time taken to locate a patch. On average an individual in a group of size n will achieve a feeding rate of

$$F(n) = \frac{A/n}{B/n + 1/C \cdot n} \qquad (1)$$

that is, an individual will eat a fraction $1/n$ only of patch A per unit time. This time span is given by a patch exploitation time shortened n times, and the time taken to locate a patch, which also becomes shortened n times. It is assumed that animals spend all their time either feeding in a patch or locating a food path. In this equation group size n cancels out and it can be seen that feeding rate is independent of group size

$$F(n) = \frac{A}{B + 1/C} \qquad (2)$$

that is, a group of size n locates a patch n times faster than an individual, but since the patch has to be divided among n individuals, the individual feeding rate is not affected by group size. Equations (1) and (2) are based on a model presented by Clark and Mangel (1986). Here we extend the basic model by considering the effects of interactions between prey, predators, and resource characteristics on A, B, and C.

Equations (1) and (2) show that group foraging as a consequence of information center-based foraging does not, without other effects arising from changes in group size, increase the mean feeding rate of individual. The benefits accruing from a larger number of animals searching for food and transmitting the information of food location at the colony vanish through the larger number of animals that the food has to be shared with. Only if A, B, or C becomes itself a function of group size n, will the

individual feeding rate be affected. Such mechanisms are not uncommon, as shown later, and some of them actually lead to an increase in the mean feeding rate. If A, B, or C becomes a function of group size n, Equation (1) can be rewritten as

$$F(n) = \frac{A(n)/n}{B(n)/n + 1/C(n)\cdot n}. \tag{3}$$

The functions $A(n)$, $B(n)$, and $C(n)$ may take the form An^i, Bn^j, and Cn^k, respectively. It becomes clear that the effect of group size on mean feeding rate only cancels out if exponents i, j, and k are of the same numerical value. This is most unlikely. Interference between individuals exploiting the patch, social factors affecting the consumption speed, information transfer within group members, and a number of other factors determine the precise value of the exponents (i, j, k). In order to understand which conditions facilitate colony-based foraging, it is useful to consider how these factors finally influence individual feeding rates in groups of different sizes, and how ephemerality and food abundance of patches affect the costs of group foraging.

A. The Effects of Patch Richness and Ephemerality

If a patch contains a large amount of food compared to the number of individuals (n) exploiting it, and the patch disappears long before competition between individuals becomes significant, an individual in a group will enjoy the same feeding rate as if feeding alone (see also Pulliam and Caraco, 1984). Patch duration is in this case primarily determined by prey ecology or other predator-independent factors, and not by the number of individuals exploiting the patch. Since food abundance is high and does not significantly decrease through the predators' actions or by their numbers ($i \cong 1$, and therefore, $An^i/n \rightarrow A$), there will be no interference between predators, and also travel times between food items within the patch stay constant ($j \cong 1$, and therefore $Bn^j/n \rightarrow B$). For rich and ephemeral food patches, in a simplified form, Equation (1) then becomes

$$F(n) = \frac{A}{B + 1/C\cdot n} \tag{4}$$

and the colony-based foragers benefit from a higher rate of patch location without an apparent reduction in the quantity of food available to the individual, and without interference between predators.

B. Predator–Prey Interference

The effect of interference between predators and prey on the amount of food available (A) in a patch is described by the value of i in An^i. If

$i = 0$, the total amount of food available in a patch is independent of group size, and the amount available per individual is A/n. If $i < 0$, there is (negative) interference between predators and prey. Resource A is not fully available and consequently the food available per individual is less than A/n. This is the case, for example, in waders (Goss-Custard, 1980) feeding upon invertebrates (e.g.. *Nereis, Corophium*). These quickly withdraw into their burrows when they sense the footsteps of waders, and the effect increases with group size of the predators. If $i > 0$, the resource A available to the predators increases with group size. As an example, this may occur if group hunting allows the capture of larger prey. Values of $i > 0$ will therefore reduce the effect of group size on the quantity of food available to each individual in a group, and values of $i < 0$ will amplify the negative effects of group size. Colony-based group foraging is more likely to occur when the negative effects of group size on the prey available per individual are low. that is, when i is rather large and positive.

C. PREDATOR–PREDATOR INTERFERENCE WITHIN THE PATCH

Interference between predators can affect patch duration B. Thus B itself can become a function of group size, that is $B(n)/n$, where $B(n)$ may take the form Bn^j. Some examples where Bn^j becomes a decreasing function (i.e., $j < 0$) of group size, and therefore leads to an increase in the feeding rate, include the cases in which animals are learning from each other where the food is to be found (Krebs, MacRoberts, and Cullen, 1972) or exploited within the patch, individuals increasing their feeding rate as a result of competition, or individuals in larger groups being able to reduce vigilance in favor of feeding time (for a review, see Elgar, 1989).

B can also become an increasing function (i.e., $j > 0$) of group size. Predator–predator interactions are more common in patches of low food densities in relation to predator density. This effect might simply appear because the predators increasingly meet the same prey item. Overall this will lead to a decrease in feeding rate with increasing group size. In the most extreme case there may be competitive exclusion at the food patch (Prior and Weatherhead, 1991b).

D. INFORMATION EXCHANGE AND PREDATOR–PREDATOR
   INTERFERENCE AMONG PATCHES

Information transfer at a colony will affect C by the fact that food patches are discovered faster if many individuals search. C itself can become a function of group size, that is, $C(n)$, which may take the form Cn^k. In the case where the information of the discoveries is diffused to

all group members (i.e., $k = 0$), each individual can derive the full benefit of group searching. Incomplete information transfer ($k < 0$) will decrease the group benefit of rate of patch location.

Predator–predator interference when searching for patches will also increase patch location time. For example, birds dispersing from a large colony in search of food patches in a relatively small area will increasingly interfere with each other (e.g., find the same patch), and therefore at large colonies the group size benefit on rate of patch location will decrease (i.e., $k < 0$).

E. GROUP SIZE, VARIANCE IN FEEDING RATE, AND RISK SENSITIVITY

The rate of patch location C increases with foraging group size and hence the time to find the next patch (1/C) decreases with group size. Large colonies will locate many patches and, assuming that information flow between individuals at a colony is high, the variance in feeding rate among individuals foraging from a large information center will be smaller than that of individuals foraging from a small one (see also Pulliam and Millikan, 1982). At an extreme, a single forager may discover a food patch rarely, but once a patch is found, food may be practically unlimited.

How will variance affect an individual's decision to participate in colony-based group foraging? If the mean expected reward of a bird in a colony of a given size meets its energy requirements, the bird is best to remain a member of the colony, that is, to be risk averse (Caraco *et al.*, 1990; Cartar and Dill, 1990). However, the individual that cannot satisfy its energy requirements should choose the risk-prone option and switch to a smaller colony, or even forage alone, as demonstrated for greenfinches by Ekman and Hake (1988).

F. INDIVIDUAL DIFFERENCES IN LOCATING AND EXPLOITING FOOD

Variance among individuals in the ability to locate patches, and variance in the ability to exploit patches, will influence the benefits of an individual that participates in colony-based group foraging. Differences in these abilities will influence an individual's decision whether to stay in a particular colony, or to leave it. As Brown, Stutchbury, and Walsh (1990) state, "certain individuals within a colony who appear to be particularly adept foragers may avoid large colonies and their attendant costs altogether, instead settling in extremely small colonies" (C. Brown, unpublished data, cited in Brown *et al.*, 1990).

In brief, an individual that can locate patches efficiently may do better

foraging alone, whereas an individual with a weak ability to locate will benefit by joining the colony and parasitizing the other individuals' ability to find patches. Information centers will be interesting for good locaters only if other benefits at the colony or the food patch outweigh the cost of information parasitism by other individuals. Similarly, an individual that is a faster exploiter than the average will benefit more from participating in colony-based group foraging than will a poor exploiter. If such differences between individuals exist, at the stable state, a colony will therefore be composed of poor locators and highly competitive exploiters, which would obviously not be a very useful information center.

G.   COLONY SIZE AND STABILITY

The information center hypothesis relies on the general assumptions that the food patches are scarce but contain an abundant food source, and that they are ephemeral (Waltz, 1982). Variance in food abundance among patches and in ephemerality will determine whether an optimal colony size can exist or not, and also influence the longer-term stability of a colony of a given size. Further, the stability of a colony also depends on how food intake, and ultimately fitness, varies with colony size. Low variance and low ephemerality will favor a stable group size and will not require much exchange of information among foragers. For the typical conditions that have been identified for the information center hypothesis, however, we do not expect colony size to be optimal or stable. High variance in food abundance among patches, plus high ephemerality of patches, will, without strong information exchange between individuals, prevent an ideal-free distribution of foragers among the patches (for further discussion, see Milinski and Parker, 1991). These conditions would there-fore favor information sampling at the communal site. This, however, requires a mechanism by which the information-sampling individuals at the colony can recognize the level of benefits that they may be able to derive at a food patch. Signaling by the successful foragers would be ideal, but is stable only if the successful forager can also derive a benefit through signaling. Such benefits can be expected and may include safety-by-numbers at the food patch, prey flushing, and others, as pointed out in Section II,C.

H.   TO SEARCH OR TO FOLLOW?

A central decision to be made by each individual in a colony is whether it should leave the colony in search of a food patch, or rather find a successful forager at the colony that could be followed to its previously discovered food patch. Clearly, the benefit of the follower strategy de-

pends on the proportion of successful searchers in a given group and is therefore frequency dependent. If all birds in a group search for food and return to the colony, a bird that decides to wait and follow instead of searching will experience short waiting times and will therefore do well. If most birds decide to become followers, only a few will search and therefore the waiting times will become unprofitably long. In contrast, ideally and without interference between searchers, the searching time for finding a patch does not depend on how many other birds search (Fig. 3A). Therefore, if an individual's net energy gain from searching (i.e., energy content of prey $[E_p]$, minus energy used up by searching and consuming prey $[E_s]$ minus energy used for returning $[E_f]$ to the information center) is higher than the energy it would have expended during waiting $[E_w]$ at the information center,

$$E_p - E_s - E_f > E_w, \qquad (5)$$

it should decide to search; otherwise it should become a follower. At a given proportion of followers and searchers the benefits of the two strategies are equal (evolutionary stable strategies, ESS; Fig. 3B); in large information centers it would not matter much whether an individual decides to search or to follow once the ESS is reached.

A fundamental difference between a roost and a breeding colony is that in a breeding colony the waiting time of a follower depends on the proportion of individuals searching, whereas in a roost the waiting time is fixed by external factors, such as tides in marine habitats, or daylength. It may be noted that the currency need not be energy for both the searcher and the follower strategy. Also, it should include other costs such as predation risk, and then be expressed in terms of Darwinian fitness.

In a recent model, Barta and Szép (1992) investigated the effects of resource characteristics on information transfer. However, in their model they fixed the ratio of searchers to followers at 1 : 1. Obviously the payoffs of the two strategies change with both their frequency and the resource characteristics, and fixation of this ratio in a model may not lead to correct predictions about how resource qualities may affect information transfer. It may be noted that the waiter–searcher model is open to cheating by non-returning searchers, and therefore does not solve the problem outlined in Section I.C. Additional benefits to searchers are necessary to compensate for the return costs.

I. BENEFITS AND COSTS AT THE COLONY

Direct benefits or costs arising at the colony will influence the decision to stay single or to join a colony. Benefits may accrue through safety from predators (Kruuk, 1964; Lack, 1968; Hamilton, 1971; Hoogland and
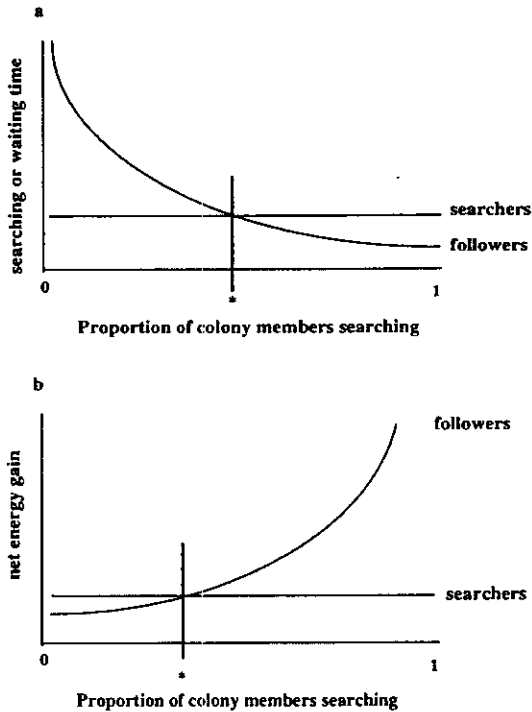
FIG. 3. (a) Waiting times of followers as a function of the proportion of colony members searching. The crossing of the curves (∗) indicates the proportion at which searching and waiting times are equal. (b) Net energy gain of individuals as a function of the proportion of colony members searching. (∗) indicates the stable equilibrium proportion where both strategies enjoy equal benefits. Both figures assume limited information transfer within the colony and no interactions between searchers away from the colony.

Sherman, 1976; Pulliam and Millikan, 1982; Pulliam and Caraco, 1984), thermoregulation (Yom-Tov, Imber, and Otterman, 1976), mate finding, extra-pair copulations (Morton, Forman, and Braun, 1990; Birkhead and Møller, 1992; Wagner, 1993), and breeding synchrony (Emlen and Demong, 1975). Costs might result from competition for mates, parasite and disease transmission (Alexander, 1974; Brown and Brown, 1986; Møller, Dufva, and Allander, 1993), and intraspecific brood parasitism and infanticide (Hoogland and Sherman, 1976; Møller, 1987; for general reviews, see Wittenberger and Hunt, 1985; Brown et al., 1990).

III. Colonial Lifestyle: Parasitism, Mutual Benefit, or Cooperation

As pointed out in the Introduction, the key problem of the functioning of colonies as information centers concerns the question of why a successful forager should return to the colonial site and thereby have to pay the time and energy cost of the trip from the food patch to the colony and back, and furthermore suffer from the costs of being followed by parasitic, unsuccessful foragers.

A. Models That Do Not Solve the Key Problem

1. The No-Cost Model

This model assumes that being followed has no costs to a successful forager, and that all individuals are free to join or not to join a colony. Since returning to the colony is costly, a nonreturning individual would, however, do better than a returning one. Thus, even if information transfer has no costs to successful foragers, the costs of returning will prevent communal roosting or breeding behavior to evolve.

2. The Unavoidable Parasite Model

This model assumes that a successful forager has to go back to the colony to bring food to its offspring and hence cannot avoid being parasitized by followers. The driving force for the evolution of communal roosting or breeding behavior is not the information transfer. Information transfer occurs simply because it cannot be economically prevented. This form of parasitism may be of importance in breeding colonies. As an example, a bird may start to breed at a site and at a later breeding stage be joined by parasitic individuals. Giving up at this stage may be more costly than being parasitized.

B. Models That Can Solve the Key Problem

1. The Reciprocal Cooperation Model

Three basic conditions are important in the promotion of cooperative behavior: (1) the costs to a successful forager of giving information have to be small compared to the benefits to the unsuccessful forager of receiving information (i.e., $F > -L$ in Fig. 2); (2) individuals that give information on one occasion must be likely to receive information on the following occasion; and (3) identification and exclusion of nonreciprocators is possible (Trivers, 1971, 1985).

We therefore expect that cooperating individuals enjoy a higher benefit than noncooperating ones. and that in this case the superior benefits from reciprocated information transfer would promote communal roosting or breeding behavior. It has recently been demonstrated that the parameter values for which stable cooperation can be expected are limited under conditions of high mobility of individuals (Dugatkin and Wilson, 1991; Enquist and Leimar, 1993; Houston, 1993). as is typical for roosts. In contrast. the exchange of information could be favored if individuals are forced into a spatial association over a longer time period. as is the case for birds in a breeding colony. The possibility that nonreciprocators could not be identified and discriminated against in large and even small colonies may exclude stable cooperation. Although the information center hypothesis has been proposed to explain the evolution of colonial roosting, stable cooperation will therefore be most unlikely to occur in roosts. However. it may arise with a low probability in breeding colonies. Although reciprocal cooperation could potentially solve the key problem, it should therefore not be expected to be an important mechanism in the evolution of coloniality.

2. A General View of Models That Do Not Require Cooperation

For an individual that discovered a food patch. returning to the colony would pay only if the payoffs at the colony (P_C) minus the costs of the flight between the food patch to the colony (L_2) and back to the patch plus the payoffs of group foraging (P_G) at the patch after the return exceed the payoffs of staying at the patch as a single forager (P_S):

$$P_C - L_2 + P_G > P_S. \tag{6}$$

For breeding, the options open to an individual are to breed singly or in the colony. The decision in favor of one or the other option is based on the exact value of both sides in Equation 6. and the colonial benefits will most likely be frequency dependent.

A single forager that discovered a food patch may additionally benefit or suffer from the effect of local enhancement at the patch (P_L), and Equation 6 then becomes:

$$P_C - L_2 + P_G > P_S + P_L. \tag{7}$$

Many factors can affect the payoffs at the colony or the payoffs from communal feeding at the food patch, as outlined in Section II: benefits at the colony arise from predator safety, thermal advantages, extra-pair copulations. and so on, and will render P_C large and positive. Benefits at the food patch arise from reduced vigilance, predator safety, social learning. and so on, and will render P_G large and positive.

Under the conditions (1) that recruiting unsuccessful foragers at the colony is more efficient than waiting for birds to join the food patch (i.e., local enhancement) or attracting other birds to the patch (i.e., local recruitment), and (2) that waiting at a colony to be recruited is more efficient than finding food alone, colonial behavior is predicted.

Two models are relevant in this context, and can offer a solution to the key problem: the generalized two-handed strategy model, and the recruitment center model. The first model promotes coloniality by rendering P_C large and positive, and the second one by increasing P_G in Equation 6.

An entirely different model is based on the benefits arising from informing genetically related individuals. This model could explain the evolution of information centers through kin selection. The functioning of these three models is presented below.

3. The Generalized Two-Handed Strategy Model

Successful foragers go back to the communal site for reasons such as predator protection, opportunities for extra-pair copulations, and thermal advantages. This possibility requires that the benefits from communal roosting outweigh the costs of being parasitized by individuals in search of a foraging site. Weatherhead (1983, 1987), in the specific two-handed strategy model, has proposed that information transfer presents the principal benefit of communal roosting for inferior foragers (e.g., subordinates), and "that the consistently successful foragers gain primarily by establishing a central roosting position buffered from predators by the surrounding subordinate birds." Therefore, the inferior foragers "buy" the information on food location by giving up safe positions in the colony to the information holder, thereby accepting a higher risk. In this model both participants can benefit, and the question of whether the net benefits accrueing to the better foragers (benefits from predator safety minus twice the flight costs to the colony), or the benefits accrueing to the poorer foragers (finding good foraging sites) are the more important selective force will depend on the relative magnitude of these two benefits.

The model does not require information transfer at the roost. Some phenotypes (e.g., adults) may have a consistently higher foraging success than others (e.g., juveniles), and therefore there is no need for the poorer foragers to be able to identify the birds that enjoyed high feeding success before arriving at the colony. They can simply adopt the rule to follow the members of the successful phenotype and by that strategy will increase their chances of finding food. Information transfer is therefore a by-product of following particular phenotypes.

4. The Recruitment Center Model

Successful foragers can derive advantages if feeding in a larger group and go to the colony for recruiting co-feeders (Evans, 1982a). The communal site therefore does function as a recruitment center for the successful foragers, and as an information center for the unsuccessful ones (Richner and Heeb, in press). Although information is transferred between birds, it is the recruitment center function of the colony that is at the origin of the evolution of communal roosting or breeding.

Mechanisms that can enhance an individual's feeding rate in a group include prey flushing, prey confusion, less need to scan for predators, and others as shown in Section II. An individual that has newly discovered a rich food patch could then increase its feeding rate by recruiting other birds. An increase in feeding rate is, however, not necessary, since it can also be beneficial to recruit other individuals to the food patch, if the predation risk at the patch thereby decreases, for example, through the dilution effect. This could be done either by recruitment at the food patch or at a colony. An individual should recruit others at the colony if this is more efficient than recruiting them at the patch. The less successful foragers should wait at the colony if this is more efficient than finding food by themselves. The successful foragers therefore use a roost as a recruitment center; the less successful ones use it as a center to obtain information about food location. Our proposition that the successful foragers use a colony as a recruitment center overcomes the difficulty of explaining why they should go to the communal roost after the discovery of an abundant food source, and explains the evolution of colonial behavior through the recruitment center function of colonies.

5. The Kin Model

In the kin model the successful forager passes the information on food location to relatives, for example, siblings, cousins, and offspring, and may therefore derive direct or indirect genetic benefits. Hamilton's rule shows that kin selection is favored when

$$rB - C > 0 \tag{8}$$

where r is the coefficient of relatedness between donor and recipient of an action, B is the benefits to the recipient, and C the costs to the donor (Hamilton, 1964). Within colonies, we identified F as the benefits to the follower and $-L$ as the costs to the successful forager arising from the time and energy expenses of the return flight plus the costs arising from passing the information to unsuccessful foragers. Informing relatives should be favored when

$$rF - (-L) > 0, \tag{9}$$

that is,

$$rF > -L, \tag{10}$$

which becomes

$$F > (-1/r)L. \tag{11}$$

The area where kin benefits arise is proportional to the degree of relatedness. Depicted in Fig. 4A is a relatedness of $r = 0.5$ (e.g., offspring or sisters in diploids). The slope of the line that distinguishes between parasitism and kin benefits is determined by $-1/r$. The cost that the successful forager is willing to pay for a given benefit to a relative increases with the degree of relatedness (Fig. 4B). As an example, the successful forager informing its sister (S) ($r = 0.5$) is willing to pay four times the
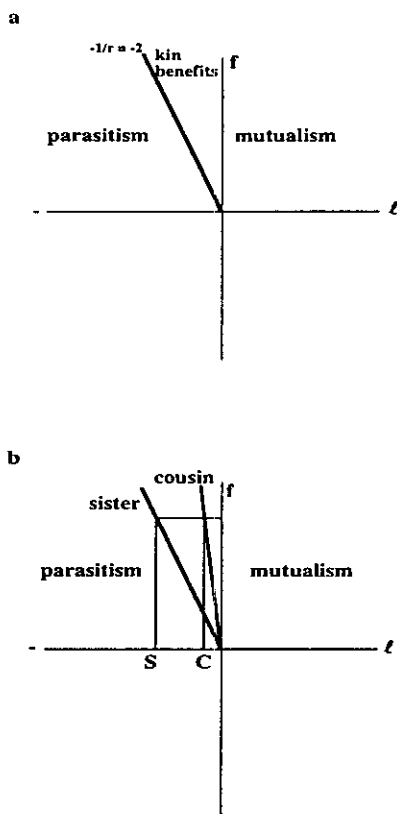

FIG. 4. (a) The costs arising to the leader can be compensated by kin benefits. (b) The costs a leader is willing to accept increase with the relatedness between leader and follower.

cost (Fig. 4B) it is willing to pay for informing a cousin (C) ($r = 0.125$). Kin benefits are probably an important reason why hymenopteran colonies function as a center of information exchange about the location of distant food patches (but see section VI,C). Among the various dispersal patterns, philopatry occurs in both colonial and noncolonial birds (Greenwood, 1980), and informing relatives could therefore provide genetical benefits to the returning bird. Inbreeding may further enhance this potential. Relatedness may also favor reciprocal cooperation between individuals as shown in roosting vampire bats (*Desmodus rotundus*) (Wilkinson, 1984). Kinship and spatial association of individuals within the roost predicted the occurrence of sharing blood meals. On any given night the number of vampires that failed to find food was high and the roles of donor and recipient frequently alternated. Wilkinson also found that the costs for the donor, in terms of time left before starvation, were smaller than the benefits obtained by the recipient.

C. LEVELS OF SELECTION

Among the models presented above, information transfer at the colony occurs in the no-cost model, the unavoidable parasite model, the recruitment center model, the cooperation model and the kin model. In the generalized two-handed strategy model information transfer may occur, but is not required. The no-cost model and the unavoidable parasite model cannot explain why a successful forager should return to a colony, and cannot promote selection for colonial behavior. Given the fact that information transfer may occur in all the other models, it is surprising that a great number of studies have attempted to test the hypothesis by using evidence of information transfer at the colony as support for the one and only information center hypothesis. The recruitment center model, the kin model, and the generalized two-handed strategy model are based on individual selection and can, theoretically, select for colonial behavior.

D. OBJECTS OF SELECTION

Concerning the four models that can potentially explain the evolution of coloniality, the objects of selection are not identical between them, and not necessarily identical between the successful and the unsuccessful foragers.

1. Generalized Two-Handed Strategy Model

In the generalized two-handed strategy model, the successful foragers are dominant birds that benefit at the colonial site by having access to positions safe from predators, or that obtain other benefits as outlined above. However, it requires that the successful foragers benefit more than

the unsuccessful, subordinate ones. In this mutual benefit model, the benefits accrue in two different currencies to successful and unsuccessful foragers, and it is therefore partly the benefits to the successful foragers at the colony, and partly the foraging benefits to inferior foragers that may select for colonial behavior. As it may be sufficient to discriminate at the colony the dominants from the subordinates, cognitive abilities to discriminate between successful and unsuccessful foragers are not mandatory, but it requires that dominance is associated with higher foraging success. The foraging benefits to subordinates may select for colonial behavior, but information transfer is not necessarily an important selective force. Colonial behavior is promoted mainly by the benefits arising at the colony to the dominants.

2. Recruitment Center Model

In the recruitment center model the successful forager benefits at the food patch by feeding in a larger group. The driving force for the selection of colonial behavior is not the benefit that unsuccessful foragers derive from information transfer, but the benefits that a successful forager can obtain at the food patch by feeding in the larger group that was recruited at the colony.

3. Cooperation Model

True cooperation based on the benefits to the individual and therefore based on individual selection is likely only if two individuals have the occasion to interact over a prolonged period of time. This situation may occur between neighboring birds in a breeding colony that raise chicks over a few weeks or months. This is the only case in which the information transfer per se over time benefits both the donors and recipients of information, and therefore the only case in which for both interactors the benefits from information transfer select for colonial behavior.

4. Kin Model

In the kin model the successful forager that passes information to his unsuccessful relatives may derive direct or indirect genetic benefits; the unsuccessful ones derive direct benefits from the information gain regarding the location of food.

IV. A Critical View of Some Predictions of the Hypothesis

In order to evaluate the information center hypothesis many studies have tested explicit predictions of the hypothesis. Most of the predictions concern the evidence that information had been transferred from success-

ful foragers to other individuals. A few problems associated with some of the predictions have already been pointed out by Mock *et al.* (1988).

A. SYNCHRONY OF DEPARTURE

The simplest prediction is that information exchange at the colony will lead to synchronous departure of birds from the colony. Clumping of departures can, however, occur for many other reasons (see, e.g., Krebs, 1978; Evans, 1982b; Bayer, 1982; Mock *et al.* 1988) and is therefore only weak support for the hypothesis. For example, food availability and prey activity may show diel or tidal patterns and promote departure synchrony. Further, the antipredator advantages of groups, the benefits arising from flying in formations, and the use of winds or thermals as means of transport may all favor clumped departures (Bayer, 1982). Social foraging by itself can provide superior ability to localize food patches (e.g., local enhancement, network foraging) and therefore also predicts departure synchrony. Further, related individuals may leave the colony simultaneously (Rabenold, 1987).

Several mechanisms that provide direct benefits from group foraging as outlined in Section II will similarly favor synchronous departure. Some examples include the cases in which the most profitable prey can more efficiently be caught by hunting as a group, or if individuals enjoy higher feeding rates as a consequence of learning from others where food can be found within the patch and how it is exploited (Gochfeld and Burger, 1982; Pitcher, Magurran, and Winfield, 1982; Krebs *et al.*, 1972). Furthermore, individuals in groups may reduce vigilance as group size increases and consequently be able to feed faster (Elgar, 1986).

In contrast, the observation of single departures cannot be used to reject the hypothesis that information has been transferred, since animals may use a precise language at the colony to communicate food location (e.g., bees, humans) and then travel singly. Or else, if the food can occur only in a few compass directions (e.g., up or down a shoreline) it is sufficient for a bird to observe the direction of departure and fly singly at a later time (Bayer, 1982).

B. SUCCESSFUL FORAGERS ARE MORE LIKELY TO BE FOLLOWED THAN UNSUCCESSFUL ONES

The prediction that successful foragers are followed by other birds more often than unsuccessful ones is widely accepted as a proof of information transfer at the colony. However, if high foraging success is associated with certain phenotypes (e.g., adults, dominants), then it is simply required

that the unsuccessful foragers are able to identify these phenotypes in order to increase their chances of finding food. Transfer of information regarding these phenotypes' previous foraging success is not necessary. This prediction is therefore of limited value, and should be used as a proof of information transfer at the colony only if it has been shown that all individuals have the same chance of finding food. This has only rarely been assessed (Brown, 1986; Wilkinson, 1992).

C. NUMERICAL INCREASE OF ANIMALS AT THE FOOD PATCH

The information center hypothesis holds that animals in a colony will find the food patch through the information provided at the colony by the discoverers of the patch. From this, some studies (e.g., Loman and Tamm, 1980; Andersson, Götmark, and Wicklund, 1981; Fleming, 1981; Kiis and Møller, 1986) derived the prediction that the number of birds at the patch will increase steeply after the discoverers return from an intervening visit to the colony. If the animals are not marked, as is the case in most studies so far, this prediction requires a few assumptions. First, it has to be assumed that most of the successful foragers also return to the previously discovered feeding site. Otherwise the newly informed birds may compensate for the ones not returning, and this would lead to no change in bird numbers, which could be wrongly used to disprove the hypothesis of information transfer. Second, it has to be assumed that there is no undetected turnover of birds at the food patch between the discovery and the subsequent revisit of the patch. If there is turnover, the number of birds at the food patch may stay constant, but many more birds know of the site than are seen at any given time. If, after a visit to the colony, all the informed birds return, it will create a steep increase in the number of birds compared to before even though no bird was informed at the colony. This effect has been demonstrated for carrion crows (*Corvus corone corone*) (Richner and Marclay, 1991). Unequivocal data to exclude turnover as the effect leading to an increase in numbers require that all birds that discovered the patch leave together, or else animals need to be individually marked to allow discrimination between the individuals that discovered the food patch by themselves and those that followed the discoverers from the information center.

Furthermore, this prediction can be used to test information transfer at the colony only if local enhancement on the way from the colony to the food patch can be excluded. For example, the animals that leave the colony for a subsequent visit to the food patch may be recognized by their way of traveling, or by other cues that allow individuals that they pass to recognize that they must be going to a good food source.

D.   INFORMATION CENTERS APPEAR WHEN FOOD IS SCARCE

Ward and Zahavi (1973) took the fact that roosts of many birds (e.g., starling, white wagtail [*Motacilla alba*], chaffinch [*Fringilla coelebs*], brambling [*Fringilla montifringilla*], red-winged blackbird [*Agelaius phoeniceus*], brown-headed cowbird [*Molothrus ater*], common grackle [*Quiscalus quiscala*], red-billed quelea [*Quelea quelea*]) (Wynne-Edwards, 1962; Moffat, 1931; Newton, 1972; Neff and Meanley 1957; Ward, 1965) become larger when food becomes seasonally scarce as one piece of evidence for the information center function of roosts. Moreover, they concluded that during these seasons the need for information is greatest, and the pool of information in the roost at its maximum.

Many bird species change their diet from invertebrate or vertebrate prey in spring and summer to plant food (e.g., seeds, nuts, berries, grain, plant matter) in winter. The diet selection model (MacArthur and Pianka, 1966; Pulliam, 1974; Krebs and Davies, 1993) predicts that of two or more food types the less profitable one (energy/handling time of one prey item) should be ignored provided the more profitable prey is sufficiently abundant. Thus

$$s_1 < [(E_1/E_2) \ h_2] - h_1 \tag{12}$$

holds (where s is the search time for prey type 1, and E is the energy content and h the handling time of prey types 1 and 2, respectively). Under this condition, prey type 2 can be superabundant and will still be ignored. If, throughout the summer and autumn, the abundance of prey type 1 decreases, the search time for this prey consequently increases until finally

$$s_1 > [(E_1/E_2) \ h_2] - h_1 \tag{13}$$

holds. At this point a sudden switch from specializing on prey type 1 to eating both prey types will occur. Since prey type 2 can at this point be superabundant, Ward and Zahavi's (1973) conclusion that during the season when birds use roosts they are in greatest need of information is not compelling. Neither is therefore the pool of information predicted to be at its maximum during that time.

It may well be that prey type 2 (e.g., berries, seeds) but not prey type 1 (e.g., arthropods) has a patchy and ephemeral distribution that promotes a colony-based foraging strategy. Whether this is the case has to be assessed. The occurrence of roosts in itself cannot be taken as evidence that roosts are used as information centers.

E.   LARGE COLONIES HOLD MORE INFORMATION

Ward and Zahavi (1973) predicted that the amount of information available in a colony increases with colony size, and it was therefore expected (Hoogland and Sherman, 1976) that unsuccessful individuals in large colonies could find a successful forager and potential leader faster than individuals in small colonies. As a consequence, individuals in large breeding colonies would enjoy a higher reproductive success than individuals in small colonies. However, Bayer (1982) argued that the positive correlation between offspring number and colony size obtained in observational studies may be unrelated to information exchange. Comparisons between colonies of different sizes are of limited value since colony size may be adapted to local conditions.

Brown (1988) predicted that the amount of time spent looking for foraging associates may decrease with an increase in colony size of cliff swallows (*Hirundo pyrrhonota*), and that consequently foraging success of individuals should increase. Brown's results showed that foraging benefits increase with colony size, and he suggested that this effect was due to a high information transfer in larger groups. This conclusion was criticized by Shields (1990) on the basis of Brown's definition of colony size, methodological problems due to uncontrolled factors that may covary with colony size, statistical problems in the sampling method, and pseudoreplication in some analyses. Shields' comments illustrate the difficulties involved in field experiments on the topic of information transfer in colonies, and point to the problems that should be considered when investigating the correlation between information exchange and colony size.

V.   EVALUATION OF THE EMPIRICAL EVIDENCE FOR INFORMATION TRANSFER AT THE COLONY

Our brief review of the literature is guided by the previous conclusions that: (1) most studies on the information center question have tried to provide evidence for information transfer at a colony, but have not tested whether the information center mechanism as proposed by Ward and Zahavi (1973) leads to colonial behavior; (2) the information center mechanism is only one among several mechanisms that equally predict information transfer at a colony; and (3) compared to the other mechanisms that involve information transfer at a colony, the information center mechanism is the least likely to explain the evolution of colonial behavior. We restrict this review to a simple evaluation of the evidence for information

transfer at a colony, but it has to be born in mind that evidence for information transfer does not allow discrimination between the several hypotheses outlined above.

Information transfer has been inferred from a variety of observations, such as departure synchrony when leaving the colony, following of successful foragers by unsuccessful ones when leaving the colony, and numerical increase of individuals at the patch after an intervening visit to the colony. Such evidence is highly insufficient and it has been pointed out a few times (e.g., Weatherhead, 1987; Mock *et al.*, 1988; Richner and Marclay, 1991) that without the use of marked individuals these observations cannot provide evidence of information transfer at the colony. Detailed observations of leading and following using marked individuals in relation to their foraging success are necessary.

Comparative approaches have also been used for evaluating the relationship between nesting type and feeding dispersion of birds in relation to their diet. Lack (1968) has pointed out that among seabirds, offshore feeders have larger colonies than inshore feeders. Krebs (1978) found an association between social feeding and colonial nesting in ciconiiformes and suggests that "it is an indication of the importance of food exploitation via an information center." Erwin (1977, 1978) compared the colonial behavior of various species of terns and found a greater tendency for breeding in colonies in species feeding further away from the nesting sites. Gori (1988) pointed out that "there is a general association in vertebrates between sociality and patchily distributed unpredictable food resources." In a recent review (Clode, 1993; but see Heeb and Richner, 1994) on the effects of predation and food resources on seabird coloniality, it was concluded that "the theory of social information centres fits the observed pattern of seabird aggregation." We rather agree with Krebs's (1978) conclusion that "post hoc interpretations of comparative evidence is not enough."

A.   Observational Evidence for Information Transfer

1.   *Mammals*

a. Bats. In evening bat (*Nycticeius humeralis*) nursery colonies consisting of females and their young, Wilkinson (1992) found that the unsuccessful foragers, as determined by their behavior and weight, gained more weight after following a successful forager than after leaving the colony singly. He concluded that unsuccessful bats could improve their foraging success by following previously successful foragers, thereby locating and exploiting richer prey patches. Bats apparently alternated between follow-

ing and leading during the course of the summer. Which cues do unsuccessful foragers use to locate successful ones?

One answer was provided by Barclay (1982). He performed playback experiments with little brown bats (*Myotis lucifugus*). using the echolocation calls of its own species but also the ones of the big brown bat (*Eptesicus fuscus*). Little brown bats approached the speaker in response to the calls of both species, and Barclay concluded that echolocation calls of bats at feeding sites (or roosting sites) could be used by other individuals as a cue for locating resources. This attraction to calls by bats is the acoustic equivalent to the visual attraction of birds to feeding flocks, and demonstrates the operation of local enhancement.

Another answer, suggested by Wilkinson. is based on the observation that successful foragers tend to urinate more after returning from a foraging trip than do unsuccessful ones. Unsuccessful bats could then use the smell of fresh urine as a cue to an individual's foraging success. It is not clear, however, how an unsuccessful forager locates a patch after leaving the vicinity of the roost. They may simply respond to the prey location calls of foraging bats, and in this case the return of successful foragers to the colony would merely indicate to the bats the temporal abundance of food. In Wilkinson's study, bats did not show strong spatial or temporal association while foraging and, in addition. there is no evidence to suggest that the unsuccessful bats followed successful ones to their food patches.

2. Birds

a. Ospreys. Greene (1987) investigated the information center question in a breeding colony of 11 pairs of ospreys (*Pandion haliaetus*) in Nova Scotia. Since ospreys carry the prey in their claws during flight, their foraging success and also the prey species brought back to the colony could easily be recorded. Greene showed that unsuccessful ospreys followed successful ones to the foraging patches. He observed that some ospreys performed conspicuous flight displays after having caught schooling fish, and this display recruited other ospreys to the food patch. Greene's result seemed to show that ospreys not only benefited through information obtained at the colony enabling them to locate unpredictable food sources but that, surprisingly, successful foragers were indicating the food type to the other individuals in the colony! Does Greene's study demonstrate information transfer at the colony?

Fleming (1990), on a visit to Greene's study area, noted that the foraging sites were visible from the colony. Furthermore, certain species of fish seemed to use predictable spawning sites. Fleming concluded that Greene's result should be interpreted as a case of local enhancement rather than as evidence of information transfer at the colony. The question

of the functional significance of the displays shown by successful ospreys remained unanswered.

Results from a larger colony of ospreys (50–60 pairs) situated inland in coastal North Carolina (Hagan and Walters, 1990) did not support Greene's result. Following of birds was independent of the leaders' previous foraging success, and ospreys seem to have individually preferred foraging sites. In summary, information transfer at osprey colonies that could indicate to unsuccessful birds the location of distant food patches (Hagen and Walters, 1990; Poole, 1989; Fleming, 1990) has not been demonstrated.

b. Swallows. Brown (1986) showed that unsuccessful cliff swallows followed successful ones when leaving the colony. This increased the follower's foraging success. All individuals were equally likely to follow or be followed. The results suggest that. for cliff swallows, colony-based foraging is beneficial. In a further study, Brown, Brown, and Shaffer (1991) found that cliff swallows hunting swarming insects call to attract other swallows to the insect swarm. These specific food calls are particularly common during poor feeding conditions. Playback experiments demonstrated that these calls can function to recruit foragers to the patch. Stoddard (1988) described a call in cliff swallows that also appeared to recruit others away from the colony. Mock *et al.* (1988) claimed that some of the social foraging benefits observed by Brown might have arisen through local enhancement since some of the food patches could have been observable from the colonies.

Studies on two closely related species. the barn swallow (*Hirundo rustica*) and the bank swallow, found no evidence for information transfer at the breeding colony. Barn swallows left the colony together but did not follow each other to the foraging patches (Hebblethwaite and Shields, 1990). Instead, they foraged singly in different foraging areas where aerial insects were abundant. Individual swallows cue in on insect-hunting conspecifics in order to locate food patches. and therefore aggregate at a food patch as a result of local enhancement rather than information transfer at the colony. In the bank swallow, both Hoogland and Sherman (1976) and Stuchbury (1988) did not observe following from the colony to food patches. Evidence of information transfer at the colony is lacking, and therefore social foraging does not seem important for the evolution of coloniality in barn swallows (Snapp. 1976; Møller, 1987; Hebblethwaite and Shields, 1990) or bank swallows (Hoogland and Sherman, 1976; Stutchbury, 1988).

c. Terns. Erwin (1978) suggested that breeding colonies of sandwich terns (*Sterna sandvicensis*) and common terns (*Sterna hirundo*) function as information centers, since terns forage in flocks over wide areas on

seemingly unpredictable food supplies. Götmark (1990) observed that sandwich terns headed off in the same direction when leaving the colony, but soon after diverged and flew to different feeding sites. Furthermore, unsuccessful foragers did not follow other birds and successful birds were not followed more often than any other birds. Even during two marked periods of food shortage, Götmark could not observe information exchange within the colonies. He concluded that in sandwich terns feeding through local enhancement is of more importance. Gochfeld and Burger (1982) have shown for the nonbreeding season that foraging sandwich terns often find feeding sites through local enhancement.

Waltz (1987) observed that common terns left the breeding colonies synchronously, and that the birds that left together went preferentially toward similar feeding areas. If the amount of time spent away from the colony was considered as an index of foraging success (successful birds return faster to the colony than unsuccessful ones), then unsuccessful birds were more likely to follow others than successful ones. Furthermore, the terns that arrived at the foraging areas in groups were more likely to catch a fish than were birds arriving alone. In Waltz's study, however, the importance of local enhancement for the foraging behavior of unsuccessful foragers was not determined (Waltz, 1987).

d. Ardeids. Overall, the results of studies on ardeid species provide little evidence of information transfer at colonies (for a review, see Mock *et al.*, 1988). An observational study by Mock *et al.* (1988) on large mixed heronries of great blue herons and great egrets did not support the prediction that unsuccessful birds should follow successful foragers of ecologically similar species (Ward and Zahavi, 1973; Krebs, 1978).

B.   EXPERIMENTAL STUDIES

1.   Mammals

a. Rats. Galef and his collaborators have investigated whether Norway rats (*Rattus norvegicus*) possess the behavioral and cognitive abilities required for food-related information transfer between individuals (see references in Galef, 1992, 1994). Norway rats are highly social animals that live in groups all year round and feed on a variety of food sources. Chemical cues found on resources (food type, nest sites) used by other rats provide a mechanism for social learning, which is used in a variety of contexts (Laland and Plotkin, 1991). Galef (1988) proposed that in most cases social learning in rats can be explained by local enhancement.

Experiments with Norway rats showed that a naïve rat can acquire sufficient information from a recently fed conspecific (the demonstrator)

to identify the food type this demonstrator ate before (Galef and Wigmore, 1983; Posadas-Andrews and Roper, 1983). Rats use olfactory cues consisting of two components: first, a diet-identifying component related to the odor of the food eaten, and second, a contextual component indicating that the food was safe to eat (Galef, Kennett, and Stein, 1985). Galef, Mason, Preti, and Bean (1988) found that carbonyl sulfide (COS) and carbon disulfide (CS_2) from the breath of demonstrator rats enhanced the attractiveness of the food they ate to observer rats. The presence of CS_2 in the food augments its attractiveness to rats (Mason, Bean, and Galef, 1989). Rats ate more than three times more food at baiting stations with food containing a solution of CS_2 than they ate at unscented baiting stations.

To test the transfer of information about the location of distant food, Galef, Mischinger, and Malenfant (1987) studied the behavior of rats following each other in a maze. They found that rats trained to follow conspecifics through a maze will follow rats that have eaten a "safe" food with a higher probability than that associated with rats that have eaten "unsafe" (poisonous) food. These results support the hypothesis that rat colonies function as information centers in which unsuccessful foragers could acquire information from the more successful colony mates about the locations of food sources, the types of food that can be safely eaten, and those that should be avoided (Galef, 1992, 1994). Galef (1991) also found that foragers mutually exchanged information about the food type they ate and this affected their later feeding behavior. Galef suggests that this information exchange among successful foragers could explain why they should return to the colony, even if they are not certain of reciprocation in the future. Recent experiments in a semi-natural enclosure suggest that rats use olfactory information transmitted by other "demonstrator" rats when choosing between two new foods (Berdoy, 1994).

2. Birds

a. Weaverbirds. Red-billed queleas, an agricultural pest in parts of central Africa, nest in colonies and may roost in groups larger than a million birds. In large aviaries, De Groot (1980) tested whether roosts serve as a center for food-related information exchange between birds. For the experiment, a communal roosting area was connected by four entrance funnels with four compartments. One group of birds was trained to find food in one of the compartments, and another group was trained separately to find water in another compartment. The evening before the experiment, the two groups were allowed to roost together. For the first test, they were deprived of food overnight. De Groot observed that the birds trained to find water followed the birds trained for food. In the

second test the birds were deprived of water and it was then observed that the birds trained on food followed the birds previously trained on water. The results suggest not only that information transfer occurred between roosting birds, but also that birds could assess the resource type that the other birds had previously accessed.

The results have been criticized (Mock *et al.*, 1988) on the argument that the birds in the roosting area could probably tell which compartment held the resource simply by measuring how long birds stay in a chamber after having entered. The results would therefore demonstrate local enhancement rather than information transfer. This criticism is, however, invalid since birds entered the compartment on the side of the roosting area, but could only leave it at the other end, which was connected to an aviary that was invisible from the roosting area. A criticism of De Groot's experiment should rather point to the fact that the birds in the roosting area could see the compartments where they were trained to find food, and could see from their roosting position where other birds entered. Hence there was no need to recognize the knowledgeable foragers at the roost, and De Groot's observation thus cannot distinguish between information transfer at the roost and local enhancement from the roost. The compartments should have been visually blocked from the roosting area in order to test whether naïve birds follow knowledgeable birds when leaving the roost. The same results would then unequivocally demonstrate information transfer at the roost.

b. Crows. The method of creating rich food patches placed randomly and remote from the colony has commonly been used to test for information transfer at the colony. Information transfer is inferred if, after a visit of a few birds to the patch (N_1), many more return (N_2) after an intervening trip to the colony (i.e., $N_2 > N_1$). Loman and Tamm (1980) created rich patches composed of dead pigs and chickens, and then counted the number of hooded crows (*Corvus corone cornix*) and ravens (*Corvus corax*) visiting these patches the first day (N_1) and early the following morning (N_2). In 13 out of 25 trials N_2 was actually smaller than N_1. Weatherhead (1987) has pointed out that these 13 trials should not be interpreted as negative evidence of information transfer but rather as failed experiments, since not all the birds present the first day returned the day after.

In 8 out of 11 trials where birds found the patch the first day, N_2 was larger than N_1. These results could be interpreted as information transfer, but even Loman and Tamm (1980) do not exclude the possibility that the effect was due to local enhancement. Moreover, the birds were not individually marked and therefore the importance of turnover of birds at the food patch on the first day could not be assessed. If birds stay for only brief periods at the patch and if they are not individually marked,

the number of birds that informed themselves at the food patch the first day remains unknown, and therefore a comparison of N_2 with N_1 becomes meaningless (Richner and Marclay, 1991). Turnover at the food patch was demonstrated for carrion crows where almost 700 birds ($\cong 20\%$) of a large population (Richner, 1989a. 1989b, 1992) were individually marked (Richner and Marclay, 1991). Because of turnover at the patch, the number of birds present at the patch at any one time during the first day was much lower than the number of birds that had acquired the information up to that time, and the results of Richner and Marclay's (1991) study were more consistent with local enhancement than with information transfer at the roost.

c. Gulls. In a breeding colony of black-headed gulls (*Larus ridibundus*), Andersson *et al.* (1981) tested the prediction that successful foragers should be followed back to their food patch by unsuccessful ones. After having successfully fed at an experimental patch, these foragers flew back to the breeding colony. Although they returned in 48 of 50 trials to the experimental patch, in none of the cases were they followed by another gull when leaving the colony. Directions of departure also indicated that other gulls left the colony independently of the experimental foragers. The result was the same when the feeding conditions in the area became very poor and following of successful foragers could have been expected. It shows that information transfer at the colony from successful to unsuccessful foragers was not relevant for food finding. Instead, some of the gulls had their preferred feeding sites, and others joined feeding gulls at their food patches. This identifies feeding by local enhancement as a prevalent mechanism for food finding.

In colonies of black-billed gulls (*Larus bulleri*), Evans (1982a) observed that some leaders produced calls that attracted other birds. Calling leaders attracted more birds than silent leaders, and leaders called more than followers. Playback experiments confirmed the attractiveness of the calls. Evans suggests that the calls serve to recruit other birds to the callers' foraging site, and that calling may be selected by benefits arising from group foraging. However, it is not clear from Evans's study why in 60% of the cases the leaders did not call when leaving the colony, and it is also not known whether the calling or the silent leaders knew the location of profitable food patches. Evans argues that birds that know the location of a food source should call as much as birds that do not know the location of food, and calling could therefore not be evolutionarily stable.

d. Wagtails. Fleming (1981) distributed a gallon of maggots over the winter foraging area of a pair of pied wagtails, which had been feeding at the food-supplemented site for a week prior to the experiment. The experiment was repeated five times involving five different (unmarked)

pairs of birds. During the time of the experiments the ground was frozen and food was probably in short supply. In none of the cases was the target pair followed by other birds the following morning. Pied wagtails commonly join overnight roosts in the winter season. However, it is unknown whether the target birds were roosting with other birds or alone.

e. Finches. Kiis and Møller (1986) provided sunflower seeds, a preferred food of greenfinches (*Carduelis chloris*), at randomly chosen sites. In 7 out of 16 trials, no bird was attracted to the patch. In the other 9 trials birds were seen feeding at the baited sites, but in only one of the cases did a larger number of birds appear at the food patch the following morning. The 16 experiments suggest that the baited sites were too poor compared to other, natural food sources. Therefore, the results are of little use even as evidence against information transfer at a roost.

f. Vultures. Rabenold (1987) tested information transfer at roosts in a partially marked population of black vultures (*Coragyps atratus*). The vultures discovered the experimental food supplement in 13 out of 30 trials, and also returned to the food in 7 of these 13 trials the following day. In the 7 successful trials, 73% of the marked birds returned to the food patch. Among the birds arriving the second day, these returning birds arrived earlier than other birds. The number of birds present increased from the first to the second day in all 7 trials, but was significantly higher than expected only in the 3 winter trials. The expected number of birds was calculated ''as the number of birds present the first day plus the same proportion of naive birds in the roost as arrived on the first day when all roostmates were naive.''

In another experiment Rabenold released 13 adult and 19 juvenile vultures that were held in captivity for 2 days, into a roost at nightfall. It was assumed that these birds did not know the current food distribution in the study area. The following morning, regardless of age, most experimental, ''uninformed'' birds left the roost later than the unhandled ones. Furthermore, uninformed birds were found at the rear of departing groups. Both observations correspond to predictions if information transfer at the roost has occurred. However, Rabenold could not exclude local enhancement as a mechanism that would also account for her results, and information transfer at the roost was not proven. She found that a demonstrably better class of food finders (adults) was routinely followed by another less capable class (juveniles) of birds. If there are persistently successful and unsuccessful foragers in a colony, there is no need for an unsuccessful forager to identify the previously successful ones. It is sufficient to follow consistently the better class in order to increase one's foraging success. In other words, information transfer regarding previous foraging success is not required.

There is evidence that in black vultures, parents and offspring maintain ties for several months past fledging, and observations show that parents continue to feed their young over prolonged periods of time (Jackson, 1975; McHargue, 1977; Rabenold, 1986). Outside the breeding season, family members participate in communal feeding and roosting behavior. Long-term associations may be mutually beneficial, and Rabenold suggests that "aid in feeding may be the largest single factor favoring retention of strong ties among members of black vulture families." Roosts may therefore serve as meeting places for family members. If related birds can benefit from food-related information exchange at roosts, then the costs of returning to the roosts may be largely compensated for by the genetic benefits given by the higher fitness accrueing to kin.

Prior and Weatherhead (1991a) investigated whether information transfer occurs at communal roosts of turkey vultures (*Cathartes aura*). In a partially marked population they tested the prediction that more birds than expected (assuming independent discovery and/or local enhancement) should arrive at the novel patches the day following the discovery of the patches. In only 3 out of 13 successful trials did more birds arrive on the day after discovery than could be expected. Interactions of vultures at the food patch suggested high competition between birds, and also monopolization of food by socially dominant individuals. This competition may limit the benefits for the birds in greatest need of food, and would therefore also reduce the benefits that subordinates could derive from following (Prior and Weatherhead, 1991b).

g. Yellow-Headed Blackbirds. Gori (1988) tested for information transfer at a breeding colony of individually marked yellow-headed blackbirds (*Xanthocephalus xanthocephalus*) by creating rich food patches of sunflower seeds and mealworms out of sight of the colony. Should information transfer at the colony occur, it was predicted that recruitment to food patches should be greater than estimated rates of recruitment by local enhancement only. This was confirmed. Gori estimated recruitment rates from local enhancement by counting the number of new birds flying in the direction where the food would be provided over a fixed period of time, and also by counting the number of birds landing and flying over the site between the time that the first bird located the site and his first repeat visit. Furthermore, the birds that returned to the food patch after provisioning their chicks at the colony were more likely to be accompanied by colony members than birds departing in other directions. In seven out of eight replicates, colony neighbors of the initial site discoverers had a significantly greater probability of being recruited to the sites than did nonneighbors. This recruitment pattern is predicted assuming that information about foraging success is more easily obtained from nearby individ-

uals than from more distant ones (Krebs. 1974). Gori (1988) concluded that coloniality in yellowheads facilitates the location of good foraging areas, and that information transfer may be implicated in this process. He suggests that unsuccessful foragers may use the rate of food delivery at the nest as a cue of who to follow.

C. SOCIAL HYMENOPTERANS

In social hymenopterans cooperative behavior can evolve via kin selection (Hamilton, 1964; see also Section III,B). The workers within a colony are the daughters of one or a few laying queens. By helping to raise their own siblings, workers increase their inclusive fitness (see review by Seger, 1991), and the costs faced by a leader returning to the colony may be offset by kin benefits.

a. Ants. Social hymenopterans have efficient mechanisms for recruiting nestmates to food sources and to new nesting sites (Hölldobler, 1977; Hölldobler and Wilson, 1990). In many ant species individuals use chemical substances as a recruiting signal by depositing an odor trail between the resource and the nest site (Wilson, 1971; Hölldobler, 1977). In the most efficient recruitment systems, as, for example, in *Solenopsis* spp., the presence of a scent trail is enough to recruit a large number of individuals (Wilson, 1971; Hölldobler, 1977; Hölldobler and Wilson. 1990). This sophisticated chemical communication system is a form of recruitment through local enhancement, where the recruited ants follow the odor trails.

Möglich, Maschwitz, and Hölldobler (1974) described the more "primitive" recruitment mechanism of *Leptothorax acervorum*. In this ant species a successful forager returns to the colony and regurgitates some of the food to nest mates. She then raises the gaster with her sting exposed extruding a droplet of liquid containing pheromones. These pheromones attract nest mates, which touch the leader on the hind legs or gaster with their antennae and then tandem running starts (Möglich *et al.*, 1974). During tandem running the leader runs in front while the follower keeps close antennal contact with the leader. The presence of a pheromone trail is not required. The two ants keep in close physical contact until they reach the food source. Tandem running is considered to be the most primitive recruitment mechanism in ants. The next step in complexity consists of "group recruitment" observed in *Camponotus* spp. (Hölldobler, 1977; Hölldobler and Wilson, 1990). In this mechanism, one ant recruits 5–30 nestmates at a time; the recruited ants follow closely behind the leader ant to the target area. In *Camponotus socius*, the scout leaves chemical cues around the newly discovered food source and lays a trail back to the colony. The pheromone trail alone does not have a recruitment

effect and the presence of a leader is essential. Hölldobler (1977) suggests that in ants. as the chemical recruitment system became more sophisticated, mechanical signals between leader and follower became less important.

b. Stingless Bees. Bees are another group of social hymenopterans in which efficient recruitment to resources has been observed (Hölldobler, 1977; Heinrich, 1978). In stingless bees, comparative studies have shown different levels of communication using recruitment techniques of varying complexity. In *Trigona* spp. recruiting signals given by returning foragers range from buzzing sounds and zigzag runs inside the hive to the laying of chemical signposts at certain intervals enabling the recruiting bee to return to the food (Hölldobler, 1977). In certain *Melipona* species leaders do not lay odor trails, but the duration of the sounds produced by returning foragers appears to vary directly with the distance to the food source (Esch, 1967). Within this system. a guide bee is generally necessary to lead up to more than fifty nestmates to the food source. When leaving a nest, leaders apparently show the direction to the goal by a short zigzag guidance flight. Competition among certain neotropical bees at their food sources appears to be one of the most important factors in their foraging strategy (Hubbell and Johnson, 1978). The ability to recruit large numbers in a short period of time enables the bees to outcompete other foragers (Heinrich, 1978; Johnson and Hubbell, 1974; Hubbell and Johnson, 1978). Compared to the honeybee, experimental studies on the recruitment mechanisms in stingless bees remain scarce. Experiments are essential to understand the details of the recruitment dynamics and the physical or chemical cues used by the stingless bees.

c. Honeybees: The Dance Language Controversy. Karl von Frisch proposed that the dances made by foraging bees from the genus *Apis* returning to the hive enabled them to recruit other bees in the hive to distant food sources (von Frisch, 1967; Lindauer, 1961). The "dance language hypothesis" proposed by von Frisch was widely accepted and became a famous paradigm in animal communication. Supporters of the dance language hypothesis claim that a honeybee colony is able to forage over a wide area because of the scouts who recruit other bees to their newly discovered flower patches by their dance in the hive. Experiments suggest that the dance effectively transmits information about the distance and direction of the food sources (von Frisch, 1967; Gould, 1975; Michelsen, Anderson, Storm, Kirchner, and Lindauer, 1992). Therefore, the honeybee colony appears to be a "classic" example of an information center with the honeybee dance as the mechanism by which the information is transferred between individuals (Seeley, 1985a, 1985b). This interpretation is not, however, accepted by supporters of the "odor search hypothe-

sis,'' who claim that food searching behavior in honeybees is much like that exhibited by other flying insects, that is, essentially based on odors (Wells and Wenner, 1973; Wenner, 1989). This alternative interpretation led to an ongoing controversy over the recruitment mechanism in honeybees (Wenner and Wells, 1990; Vadas, 1994). The odor search hypothesis is a more parsimonious mechanism for food finding in bees and does not require the exceptional cognitive capabilities assumed by the dance language hypothesis (Wells and Wenner, 1973; Wenner and Wells, 1990; Wenner, Meade and Friesen, 1991; Vadas, 1994). According to supporters of the odor hypothesis, the experiments carried out by the dance language proponents appeared to be flawed in various respects. They point out that the dance language researchers usually concentrated their attention on the bees effectively recruited by the dance, while the majority of bees foraged without apparently using it (Wenner and Wells, 1990; Wenner *et al.*, 1991). Furthermore, they found that most bees searched for food, water, and new hives close to their home hive, where the information obtained through the dance would be of little use (Wenner *et al.*, 1991; Vadas, 1994), and the time taken by recruits to find the food patches was greater than would be expected if the dance informed them of the location and distance of the food patches. As a way out of this controversy, Wenner *et al.* (1991) proposed that instead of concentrating on one single hypothesis, honeybee researchers need multiple working hypotheses in the context of a ''strong inference'' approach (Platt, 1964). In a review of the controversy, Vadas (1994) suggested that instead of assuming a priori the importance of the dance language, it has to be determined in what circumstances dances and/or odors are important for recruiting bees to food and other resources.

In summary, both hypotheses appear to be relevant in honeybee recruitment and there is little doubt that the beehive functions as an information center. The challenging question is whether coloniality in bees originally evolved through the benefits of information exchange *per se* or through the benefits of information exchange between kin only.

D.   CONCLUSIONS FROM THE EMPIRICAL EVIDENCE

Evidence that colony members exchange information concerning the location of distant food patches is scant. This is even more pronounced if one considers the large number of studies conducted over the past twenty years that were designed to test information transfer. Many studies were purely observational, most studies used unmarked animals requiring specific assumptions, and in much of the work the simpler mechanism of foraging by joining animals at their food patch (i.e., local enhancement)

could not be excluded. Furthermore, other hypotheses that make the same predictions as the information center hypothesis were in most cases not even considered. The lack of empirical support makes it unlikely that the function of roosts and colonies as information centers is of much importance for the evolution of colonial behavior.

VI. Summary

The evolution of coloniality in birds, mammals, insects, and other species is still a riddle. In contrast to the hypothesis of Lack (1968) that the antipredator function of bird roosts and colonies led to the evolution of colonial behavior, Ward and Zahavi (1973) reached the conclusion that communal roosting and breeding in birds has evolved for the exploitation of patchy food sources. This is now known as the information center hypothesis.

The information center mechanism holds that individuals at the colony exchange information about the location of distant food patches, and that a foraging individual that is unsuccessful on one occasion can follow a successful individual from the colony; when it is successful it will be followed by unsuccessful ones when leaving the colony. The hypothesis rests therefore on the assumption that the individuals participating in an information center benefit and lose in turn, and by chance. The altruistic act of an individual is expected to be reciprocated by others in the future. The information center hypothesis further claims that this information transfer was the main selective force for the evolution of coloniality. The key problem of the functioning of colonies as information centers concerns the question of why a successful forager should return to the colony and thereby pay time and energy costs of food trips and parasitization by unsuccessful foragers. Without reciprocated cooperation, the originally proposed information center mechanism rests on group selection.

Although the reciprocal cooperation model satisfies the evolutionary criterion that selection should be based on benefits to the individual, the stringent conditions posed by cooperation models and the high mobility of animals in colonies will most likely preclude stable cooperation between individuals in colonies.

Several other models that will favor colonial behavior, and are based on individual selection, do not require reciprocal cooperation: the generalized two-handed strategy model (successful foragers return to the colony for the benefits they obtain by communal roosting or breeding), the recruitment center model (successful foragers benefit at the food patch by communal feeding and return to the colony for recruiting other foragers), and

the kin model (successful foragers return to the colony to inform kin about the location of food patches and thereby benefit by increasing their inclusive fitness). Information transfer will occur in the recruitment center model and the kin model, and may occur but is not required in the generalized two-handed strategy model. However, in all three models it is not the information transfer to unsuccessful foragers at the colony that is at the origin of the evolution of colonial behavior, but either the benefits that the successful foragers derive at the colony (in the generalized two-handed strategy model) or at the food patch (in the recruitment center model), or the benefits to the successful forager from promoting its genes through helping kin (in the kin model). Nevertheless, in empirical studies the occurrence of information transfer between successful and unsuccessful foragers was thought to be sufficient evidence for the information center model, thus ignoring all other models where information transfer is also predicted. It is therefore not surprising that a review of many observational and experimental studies provides nearly no support for the information center model. Many predictions of the information center model cannot be upheld and, partly because much research was centered around a single hypothesis, research into the evolution of colonial behavior has stagnated.

In our review, we (1) analyzed the costs and benefits of colony-based group foraging, (2) analyzed the levels and objects of selection of the various models that can lead to coloniality, (3) examined some common predictions of the information center model in the light of recent theory, and finally (4) evaluated the empirical evidence for information transfer at the colony. We propose that the original information center hypothesis for examining the evolution of coloniality should be abandoned in favor of the promising alternative hypotheses that are explicitly based on individual selection.

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