

SIMULATION AND ANALYSIS OF INFORMATION-CENTER FORAGING

by

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(With 8 Figures)

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Summary

I present a mathematical model and simulation of information-center (IC) foraging (WARD & ZAHAVI, 1973). The results indicate that the most important condition for supporting an IC is time-limited foraging in patches supporting multiple individuals. Foraging rate is enhanced by information exchange even where the probability of finding food is otherwise relatively high (*i.e.* not, as generally assumed, exclusively where food is "unpredictable"). The effects of IC foraging are strongest for small populations ($N < 20$), though they increase marginally as the number of individuals increases. One can determine the critical patch-duration at which IC foraging becomes profitable and how individuals may optimally distribute search time between active scouting and vicarious search (through recruitment in the IC). As food becomes difficult to find, the optimal proportion of time an individual should scout on its own approaches roughly one-half.

Introduction

The information-center (IC) model of foraging (WARD & ZAHAVI, 1973) suggests how a colony or hive can not only serve as a common, central location for foraging bouts, but how information about the location of food can be transferred from one forager to another. Information can be conveyed (intentionally or not) in the form of flight direction (to or from a foraging site - birds), pheromone or odor trails (ants, termites), or odors and "dances" (honeybees). Such transfer of information between individuals at a central site, along with population-level response, has been reported among insects (honeybees: VON FRISCH, 1967; LINDAUER, 1971; WENNER, 1971; SEELEY, 1985a; WENNER & WELLS, 1990; ants and ter-

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mites: WILSON, 1971) and many birds (cattle egrets: SIEGFRIED, 1971; great blue herons: KREBS, 1974; crows and ravens: LOMAN & TAMM, 1980; weaver birds: DE GROOT, 1980; cliff swallows: BROWN, 1986, 1988; osprey: GREENE, 1987; common terns: WALTZ, 1987; but see also MOCK *et al.*, 1988).

Despite the occurrence of IC foraging in diverse groups, however, there has been little theoretical treatment of the model. WARD & ZAHAVI (1973) and others (ERWIN, 1978; WITTENBERGER, 1981) regard the information-center strategy as an adaptation for exploiting "patchy" and/or unpredictably distributed food. They regard the transfer of information as increasing the probability of an individual finding food, implicitly suggesting that this is done with little or no cost. This assumption has not been thoroughly examined theoretically. KREBS (1974), WALTZ (1987) and BROWN (1988) have assessed the social benefit to individuals where an IC strategy is used, and ERWIN (1978) and BROWN (1988) have measured how factors such as colony size in IC situations relate to individual foraging rate. I expand on the extant studies (above) by addressing more generally how the parameters involved in IC foraging (such as predictability of finding food in the environment, investment in search time, colony size, patch richness and patch duration) affect both the probability of an individual finding and individual foraging rate. In particular, I ask: under what circumstances can IC behavior increase foraging rate? (In cases where the time available exclusively for foraging is given, the question may also be expressed as: what increases total amount foraged?) If "patchiness" is critical, for example, at what value(s) does it contribute significantly to foraging rate (or total amount foraged) and thereby allow individuals to profit by using an IC? I also consider how the optimal percentage of time spent scouting can be shaped by an information-center.

The model and simulation

First I consider a model that examines how the interaction of many individual foragers affects what would otherwise be individual foraging rate. To highlight how an information-center can affect the individual's probability of finding food, I do not consider the absolute density of patches or prey items, or the organisms's perceptual apparatus or environmental cues that an individual might use to locate food. Rather, I assume that these factors can be telescoped into one value — a probability that an individual forager will find a patch of food in a given unit of time

(further conditions for patch richness implicit in this value are discussed below under collection). The model then asks how this base probability is modified in an information-center.

One needs first to recognize two sequential components of foraging: (1) search and (2) collection (pursuit, manipulation, *etc.*). Search can often be negligible in terms of energy or time invested relative to collection (STEPHENS & KREBS, 1986, p. 36), but I am aiming to address in particular those cases in which search time may be significant in overall foraging behavior. The information-center foraging strategy is, in fact, presumed to be effective when foraging is search-limited — that is, where “information” about the location of food can be valuable. Overall foraging rate, f , is thus the amount of food collected, F_{collect} during time spent both searching (T_{search}) and collecting (T_{collect}):

$$f = \frac{F_{\text{collect}}}{T_{\text{search}} + T_{\text{collect}}} \quad (1)$$

Below, I discuss how search and collection can each be addressed individually, and then I briefly describe how the two components are combined in the simulation.

1. Search.

Consider an individual allocating its time solely within the context of search. First, an individual in an information-center may spend all its time actively searching on its own until it finds food: what may be labeled as “scouting”. The probability that it will find food may be designated as:

p = the chance of an individual locating a patch in one time unit.

Mean search time under such conditions of continuous scouting will be $1/p$. Where there is an information-center, however, an individual can follow other strategies. As a second strategy, it may search using only the information available through other foragers (intentionally on their part or not), thereby relying wholly on others to locate food: what may be called (after CAMPBELL, 1974) “vicarious search”. The probability of finding food via other individuals will be based, first, on:

N = the number of individuals that might provide information directly that is, the size of what may be termed the “neighborhood”. The relevant neighborhood of individuals may be the whole colony, where all individ-

uals have visual or other contact with each other (*e.g.* osprey, cliff swallows), or it may be a more local subset of the population (*e.g.* honeybees in one section of a hive). Vicarious search will also depend on the percentage of other individuals actively scouting, based on:

s = the proportion of time each devotes to its own scouting.

Finally, vicarious search will be based on the probability, p , that each finds food. The rate of scouting failure for each will be $(1-p)$ and the collective failure of sN individuals, assuming the scouting bouts are independent, will be the product of their separate failures: $(1-p)^{sN}$. The rate of collective success - the probability of a waiting individual "finding" food vicariously - is thus:

$$P_{\text{vicarious}} = [1 - (1-p)^{sN}] \quad (2)$$

The third search strategy is a hybrid of distributing time between vicarious search (waiting) and scouting (actively). I am concerned here with cases where all individuals in a population follow the same strategy - namely, devoting a certain proportion of their search time to individual scouting. In a hybrid strategy, the individual devotes s time, as defined above, to scouting and $(1-s)$ time to waiting, with the overall probability of finding food:

$$\begin{aligned} P_{\text{hybrid}} &= sp + (1-s) (P_{\text{vicarious}}) \\ P_{\text{hybrid}} &= sp + (1-s) [1 - (1-p)^{sN}] \end{aligned} \quad (3)$$

The first two search strategies (above) may be expressed as special cases in which for exclusive individual scouting, $s = 1$, and for exclusive vicarious search, $s = 0$. Again, the search time, T_{search} (as it contributes to overall foraging rate, eq. 1) will be $1/p_{\text{hybrid}}$.

The IC search strategy expressed in equation 3 has several interesting features (refer to Fig. 1). First, individuals can reduce their own search time (thereby increasing foraging rate - eq. 1), while not decreasing the group's collective chance of finding food. For example, an individual may attain the same base probability, p , by either scouting constantly ($s = 1$), or by scouting only its "share" of the time among those individuals in the neighborhood where information is exchanged ($s = 1/N$; see Fig. 1). In addition, however, the probability that an individual finds food in the IC (p_{hybrid}) can be increased above what one individual can achieve searching (scouting) alone (p). For each pair of p and N , there is one maximum, which may be referred to as p_{max} . (There is, however, no closed, mathematically explicit solution for p_{max} given eq. 3). The value of p_{max} reflects the maximum contribution of information sharing (via reduction of

search time) to foraging rate (in the context of search only - see below for qualifications imposed by considering collection also).

The percentage of individuals scouting at any given time, s , is a conspicuous and fundamental property of an information-center (*e.g.* SEELEY, 1983, 1985b, for honeybee hives; BROWN, 1986, for cliff swallows). Because an individual forager cannot both scout away from the IC and acquire information at the IC simultaneously, the percentage values in Fig. 1 represent a strategic choice or balance between the two alternatives. Allocating search time between waiting and scouting according to some fixed ratio is, of course, only one possible search strategy that may account for the ratios observed by SEELEY and by BROWN.

2. Collection.

Individual collecting rate may be affected by many specific physiological or ecological factors, but I do not consider them in the model. I assume that individual organisms have a mean overall collecting rate and, further, that this rate is not affected by information transfer (including possible crowding at the patch). Rather, the relevant parameters include, for example, how extensively or rapidly foragers are recruited to a site, how much food a patch contains and how long the patch persist.

Because search is treated separately, one may regard collection as simply "harvesting" according to some uniform mean rate (in other contexts, where search is not addressed, this may be viewed as the complete foraging rate). In such cases, collecting may be limited by:

R = patch richness (the amount of food available per site).

Alternatively, where, say, tides, carcass decomposition or flowering time are relevant, collection may be limited instead by:

D = patch duration (the period of time that it is available).

The limiting factors for collection indirectly determine (based on an assumed collection rate) how long food can be collected (T_{collect}) and how much can be collected (F_{collect}). When combined with the corresponding search time, they also determine net foraging rate (eq. 1).

Because IC foraging by its nature involves multiple foragers and often multiple visits, foraging rate is best analyzed on a very coarse-grained level. I take as the basic unit of collection one complete bout or foray in which the forager returns with, say, a full load of food. A characterization of foraging in terms of full-loads is especially apt where foragers return intermittently to a nest, colony or hive with food for others — for

example, in a breeding bird colony where parents feed offspring, or in an insect hive or colony, where specialized foragers feed non-foraging castes. In many cases where information-center foraging has been reported, in fact, the return of a forager with a full-load has been the "informational" basis for others to follow on successive forays. Patch richness, then, is expressed here in terms of individual full-loads or multiples of the amount that can be collected during one foray or foraging bout. A patch whose richness is 10, for example, can accommodate one individual for ten time units (bouts or forays) or ten individuals for one time unit. Patch duration may likewise be expressed in units of time during which such full-loads are collected. This form of expression also means that the relationship between the amount of food collected and collecting time is a factor of one: one full-load implies one time-unit to collect, and vice versa.

Where an individual forages on its own, collecting time and the amount of food collected each directly reflect the patch richness (or duration), R (or D). Where an individual forages via an information-center, by contrast, other foragers follow or are recruited to a patch and the total amount of food is distributed among many individuals. Though some arrive to the patch early and some late, one may assume that in the long run, over many patches, the differences in arrival times cancel and food is shared evenly by those collectors that reach a site. In many cases, this will involve all the individuals in the initial search neighborhood, and (where collection is richness-limited) the individual food collected, F_{collect} will be R/N .

The specific rate of following or recruitment will strongly affect collecting time (and in some cases, also the amount collected). As foragers congregate at a site, they deplete the patch more quickly. This reduces the collecting time (and the amount) per forager. Recruitment rate may be especially significant where collection is limited by patch duration rather than by patch richness. That is, the recruitment rate will determine how many individuals can actually reach and exploit a patch before it becomes unavailable again.

Recruitment and vicarious search reflect the same information transfer viewed from opposite ends. Thus, if sN individuals are scouting in a given time unit, $(1-s)N$ individuals are recruitable. In successive time units, the individuals at first unrecruited will be recruited gradually and increase the total number collecting at time t , C_t :

$$C_t = N(1-s^t) \quad (4)$$

From the recruitment equation (for the number of individuals collecting

at each successive time interval), one can determine (by integration) the equation for cumulative forage (see *e.g.* Fig. 6 below). Given the patch richness as well, one can determine how quickly a patch will be exhausted (T_{collect}) and the final number of foragers (and, therefore, F_{collect}). If collecting is interrupted instead by the loss of the patch at some time, t , one can determine from the recruitment function the number of individuals recruited and the cumulative amount foraged. The recruitment function, as a direct correlate of the proportional time spent scouting, is central to foraging rate in an IC.

Alternative recruitment strategies are possible, just as there can be alternative search strategies. For example, the neighborhood within which information is transferred may be local, but information about profitable patches may also spread through overlapping neighborhoods to all individuals in the population. In such cases, information may spread geometrically from one center (say, from one nest in a bird colony, with a steadily increasing radius: $C_t = Nt^2$; compare to eq. 4). Information may also spread logistically through a randomly mixing population (*e.g.* in an ant colony). Recruitment may thus follow several patterns, but the number of foragers in each typically increases with time, producing a growing rate of patch depletion (again, assuming collecting rate itself is uniform). There is also a limit to recruitment, the population size, which sets an upper bound on the rate of patch depletion (corresponding to a lower bound on the collecting time, R/N). If the patch persists, then for the individual (because $1 \leq C_t \leq N$): $R/N \leq F_{\text{collect}} \leq R$ (measured in full-loads), and $R/N \leq T_{\text{collect}} \leq R$ (measured in full-load bouts - see above).

3. Combined simulation.

Because of the number of parameters involved and the complexity of their interaction, there can be no analytic treatment of combined search and collection. As presented above, search in an information-center is shaped by p , s and N ; collection by R (or D), s and N . The two components of foraging are also related through the parameters of information exchange. Together, s , the individual scout percentage, and N , neighborhood size, determine both search and recruitment patterns in IC foraging.

The interaction of search and collection is also somewhat paradoxical on the surface. That is, an increase in the availability of information per individual decreases search time and increases foraging rate (eq. 1); at the same time, however, it also leads to more rapid spread of information,

greater recruitment and less food collected per individual, thus decreasing foraging rate. Simulation can resolve this.

The simulation used here also allows for some stochastic process - for example, in finding food where predictability is very low (where $p_s N < 1.0$) and in rounding off "fractional" individuals where the number of total foragers is low (where $sN < \sim 5-10$). In addition, multiple sites can be discovered and exploited simultaneously.

Results and discussion

1. Search.

Figure 1 shows how an information-center can indeed increase the probability of finding food. By reducing absolute search time, individuals also simultaneously reduce the amount of energy they invest in search. The

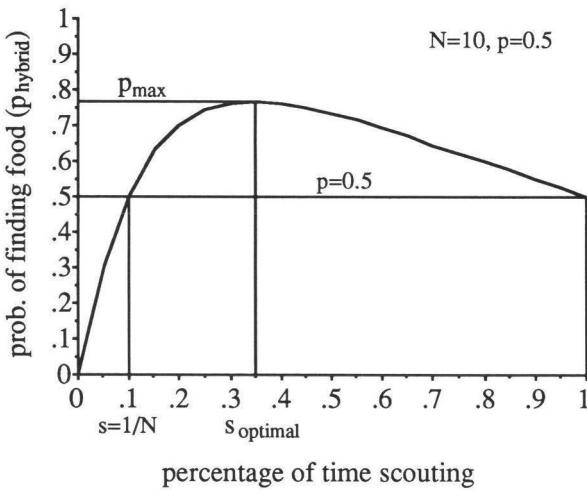


Fig. 1. Probability of finding food for different hybrid strategies. The probability for an individual searching alone (here, $p = 0.5$; $s = 1$) can also be achieved collectively by each individual searching its share of the time (in a neighborhood of size N , when $s = 1/N$). There is one maximum, P_{max} , associated with a proportion of time scouting, $s_{optimal}$.

contribution to net foraging rate (eq. 1) is better evaluated here, though, in terms of the "relative search time", the ratio of the (minimum) time for an individual in an IC to the time for a comparable solitary forager: $1/p_{max} \div 1/p$. As food becomes more difficult to locate, in fact (*i.e.* as $p \rightarrow$

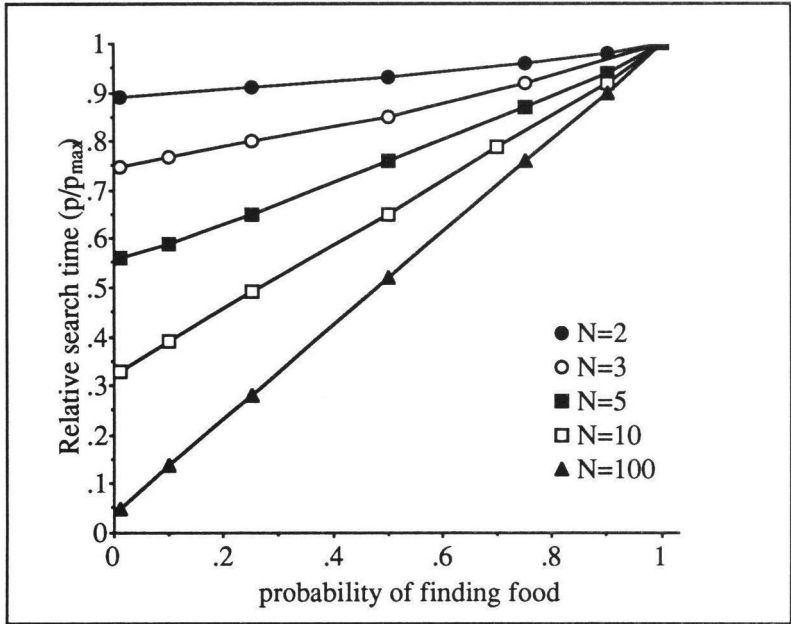


Fig. 2. Relative search time *vs* probability of finding food. Relative search time can be decreased as food becomes more scarce. Relative search time can also decrease as neighborhood size (N) increases (see Fig. 3).

0), relative search time can decrease substantially (Fig. 2). The relationship is nearly linear (corresponding to a *geometrically* increasing contribution of p to foraging rate).

Neighborhood size, N , can also affect the probability of finding food. As the number of individuals that can provide information increases, the relative search time also decreases (successive curves in Fig. 2; more clearly depicted in Fig. 3). For larger N , the relative probability of finding food (*e.g.* Fig. 1) can increase manyfold as food becomes more unpredictable (for example, where $N = 20$, $p_{\max}/p \approx 5$; for $N = 100$, $p_{\max}/p \approx 25$). As N increases, the *absolute* probability of finding food approaches unity, even where food is difficult to find for a non-social individual (for example, for $N = 100$, $p_{\max} = 0.95$ where $p = 0.5$; for $N = 1000$, $p_{\max} = 0.95$ where $p = 0.1$). There are thus limits to the relative search time (asymptotes in Fig. 3).

There are limits, however, to the potential benefit of viacrious search through an information-center. Figure 2 shows, for instance, that (for a

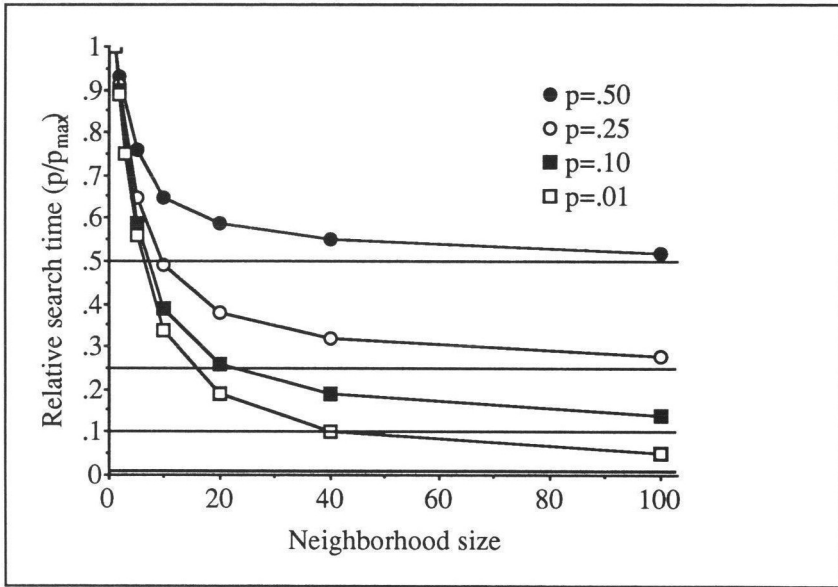


Fig. 3. Relative search time vs neighborhood size. The decrease in relative search time occurs most dramatically for small N. There is a limit to the possible decrease in relative search time for each base probability of finding food (p) as $p_{max} \rightarrow 1$ (asymptotes occur where $p/p_{max} = p$).

given neighborhood size) as food becomes scarce, there is a limited reduction in relative search time. Figure 3 shows that while increased neighborhood size also can reduce relative search time, there are limits (asymptotes). This occurs where the value of the relative search time due to hybrid searching equals the value of the individual's probability of finding food in the environment. For example, where the chance of a single individual locating food in one search bout (or unit time) is one-half, an individual cannot reduce its search time in an information-center by more than one-half.

One may also note that the sharpest reductions in relative search time derive from the first few available sources of information (*i.e.* where the local neighborhood is small; Fig. 3).²⁾ Virtually half the potential reduction, for instance (regardless of base probability), can be achieved with a neighborhood of as few as five other individuals. Large-scale reductions in

²⁾ When graphed on log-log scale, Fig. 3 shows negative sloping sigmoidal curves (with inflections at $1/p_i$).

search and therefore in foraging time may result from large numbers of individuals in a colony, hive or other information-center, but the most significant reductions in search time are contributed by the first few individuals. In fact, as Fig. 3 shows, the reduced time due to additional individuals can be quite marginal as N increases.³⁾

Isolated analysis of search time thus indicates that IC foraging is beneficial (reduces relative search time) because of the nearly direct function of the decreasing probability of finding food (Fig. 2); this suggests that any selective advantage of IC foraging does not occur exclusively where "predictability" of food is low. Also, the advantages of IC foraging for search are available even where the number of individuals is low. This suggests that an IC strategy could originate even in a small group; further, the relative value of the IC would increase only marginally as the population size increased.

2. Scouting strategy.

Figure 4 shows how time is optimally apportioned in a hybrid strategy (eq. 3) between scouting (individual search) and vicarious search (waiting) as p and N vary. Optimal scouting time is relatively sensitive to changes in the predictability of food in the environment when N is large (and p is low). On the other hand, when N is low, it is more sensitive to changes in the size of the IC neighborhood itself (successive curves in Fig. 4). With respect to neighborhood size (Fig. 5), the reduction in an individual's proportion of time scouting occurs most dramatically where N is small. That is, again, the effects of an IC appear even with few individuals (say, the first individuals evolving social from solitary foraging). The optimal scouting percentage, s , ranges widely, but does not become low (< 0.1) except where N is large (> 30). Even so, as food becomes more unpredictable for large N , the optimum approaches 0.5 (Fig. 4). That is, an optimal strategy where food is extremely "patchy" or unpredictable requires an individual to scout generally half the time. Though the probability of finding food increases substantially (Fig. 2), there is not a corresponding decrease in time an individual must "invest".

³⁾ This result is related in part to the assumption above that individuals do not coordinate their search and that the probability of each forager finding food is independent of the others. While several researchers have observed that information about successful foraging sites has been conveyed in nature, they have not also reported that information about the locations of unsuccessful search is also conveyed.

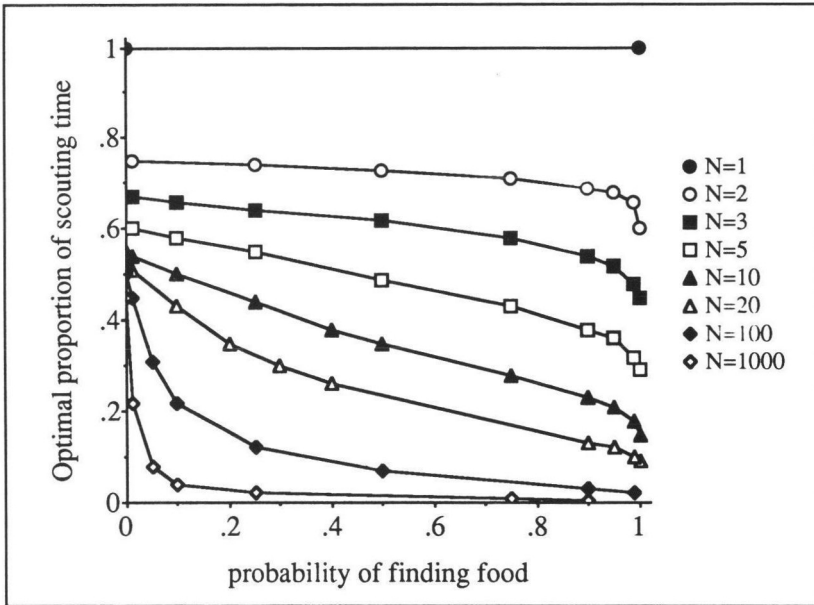


Fig. 4. Optimal proportion scouting time vs probability of finding food. Note that as food becomes scarce, optimal proportion of scouting time approaches roughly 0.5, even for large neighborhood size (N).

3. Collection.

According to the model, IC foraging is significantly shaped by patch size and patch duration (the factors that limit collecting). As WITTENBERGER (1981) noted, for example, cursory inspection of the dynamics reveals that the patch must remain long enough for recruitment to occur (in the language of the model, $D \geq 2$). More importantly, though, because food is shared, a single patch must be rich enough to provide a surplus ($R \gg 1$, measured in full-loads). Otherwise, sharing information would quickly reduce the already limited food; one would expect to find selective mechanisms that suppressed the display of information or guarded against its use by others. WEATHERHEAD (1983) has suggested, in fact, that certain birds in a colony are merely parasitic on others and that one must look for compensatory benefits, such as the buffering from predation provided by the surrounding zone of the followers' nests. In some cases, however, recruitment appears to be "deliberate", as in ospreys that give calls and exhibit dramatic undulating flight (GREENE, 1987) or in honeybees that

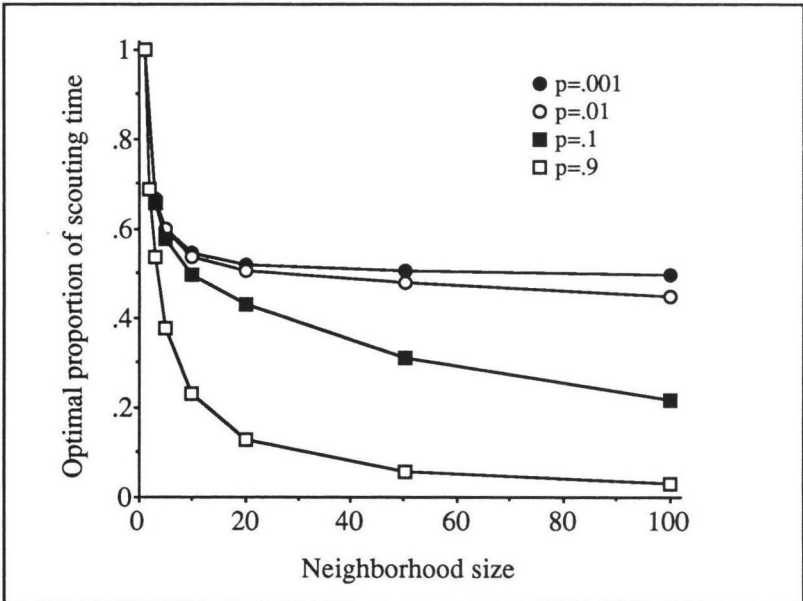


Fig. 5. Optimal proportion scouting *vs* neighborhood size. Reduction of individual search time occurs most dramatically for small neighborhood size (N).

“dance” (VON FRISCH, 1967). For an IC strategy to be effective, mean patch richness must be able to accommodate multiple foragers per site.

Recruitment, however, regardless of its rate, poses a further problem. That is, each additional forager dilutes the total food potentially available to a solitary forager in one patch, given indefinite time to collect it. The more individuals (*i.e.* due to greater information exchange and recruitment), the more the dilution. The deficit incurred by sharing food (say, with N individuals, receiving an average of only R/N each) can only be balanced in the long run by an equal increase in the number of patches visited (in this case, by a factor of N in the frequency of finding food: $p_{\max} \geq Np$). But while sharing information about sources of food can increase the rate of finding food (*e.g.* Fig. 1), it cannot increase it by more than the number of individuals involved (to achieve that limit, searches cannot be even partially redundant - unlikely, as suggested in note 2). Collection may be limited by other factors, however. As long as the periods during which patches appear remain brief enough, then the possible limits introduced by additional foragers will not be reached. This resolves, in a sense, the paradox of recruitment (above): where collection is time-limited,

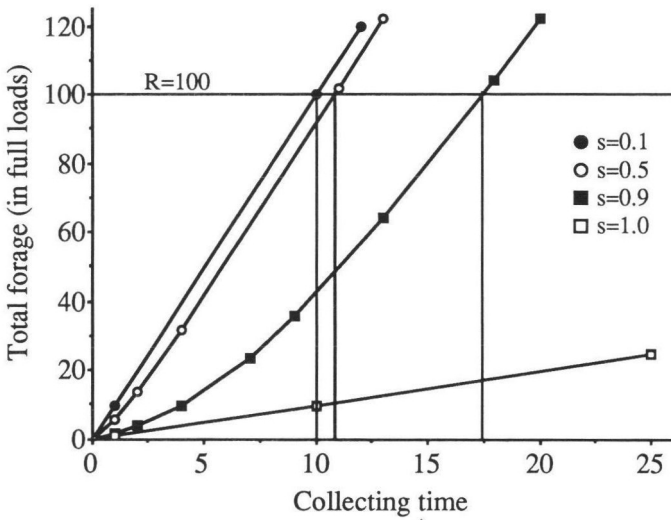


Fig. 6. Cumulative forage vs time (sample where neighborhood size = 10). As proportion of time spent scouting by each individual (s) decreases (and waiting period increases), initial recruitment occurs more rapidly. Foraging rate (also patch depletion rate) reaches an upper limit when all foraging individuals in the population have been recruited. Critical patch duration (the time before which collection is time-limited) can be found by noting the time where the collecting curve reaches a given patch richness (here, where $R = 100$).

increased information exchange increases the ability to collect the food before it is gone. For IC foraging to operate by enhancing foraging rate alone, food must be “patchy” in both space and time (concentrated into patches rich enough for multiple foragers and, at the same time, into periods short enough that even a group of recruited foragers cannot exploit the patches fully).

The degree of temporal “patchiness” commensurate with IC foraging is determined by the “critical patch-duration”, the time at which a patch would otherwise be exhausted by recruited foragers.⁴⁾ Up to this time, any interruption of foraging or loss of food availability cuts off collection before the full potential is reached (*i.e.* collection becomes limited by time). Again, this can be determined for a given information-center from the recruitment function (eq. 4, or variant thereof). Figure 6 displays a sample series of collecting curves for different recruitment/scouting rates;

⁴⁾ The significant time period — and also the one most readily measured in the field — begins with the onset of foraging (*i.e.* one need not have absolute data about the duration of patches or know how long a patch has been available before being found by a forager).

it shows that the critical patch-duration time decreases as information is more widely conveyed or dispersed (as $1-s$ increases, or as s decreases). The shortest critical period (were $s \rightarrow 0$) occurs where collecting reaches its maximum rate (introduced above): at $D = 1 + (R-1)/N$ (where R is very large, $D \cong R/N$). The critical patch-duration also shortens as the number of individuals, N , increases (increasing recruitment rate), and lengthens as the richness, R , increases (available food increases). Crowding effects, where they occur (not considered formally here), would tend to reduce the effective richness of the patch and thereby decrease the critical patch-duration. Even with crude figures about patch richness and recruitment (available empirically), one can estimate the time that according to the model limits patch availability in an information-center (see § 5 below for potential further studies).

4. Combined simulation.

The results from the simulation mostly follow those for search and collection considered separately. For example, where patch-duration (D) is not limited, foraging rate decreases as neighborhood size increases, due to the uncontrolled sharing of food (Fig. 7). Without temporal patchiness (patch-duration below its critical value), foraging rate is lower for individuals in an information-center.

Foraging rate in an IC can increase (relative to solitary foragers) when collection is time-limited, depending on neighborhood size and how individuals distribute time between scouting and vicarious search (s). Figure 8 shows foraging rates for a series of neighborhood sizes (for a sample set of values). An individual's IC-foraging rate exceeds the solitary rate (horizontal line) for a range of hybrid search values. In some cases, foraging rate will be lower either because scouts find patches too infrequently to offset the sharing of a limited amount of food (low s) or, alternatively, because the recruitment of individuals is too slow to exploit a time-limited patch (high s , especially for low N). In each case, there is, once again, an optimal proportion of time for an individual to spend scouting. Due to slower recruitment at high s , the optimal values are slightly lower ($\Delta s \cong -0.05$) than those predicted by considering search alone (Fig. 4). The foraging rate is relatively insensitive to variations in s around the optimum (note the flat shape of the curve at its peak, Fig. 8). An individual's scouting behavior may thus fit in a fairly broad range of s values, while still approximating the largest potential increase in foraging rate: one might not expect the value of s to match the optimum precisely.

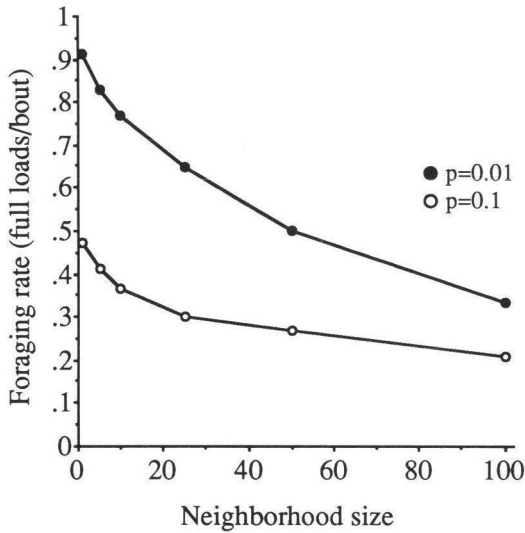


Fig. 7. Foraging rate vs neighborhood size. Combined simulation shows that foraging rate decreases where collection is not time- or patch-limited (two samples with different probabilities of finding food).

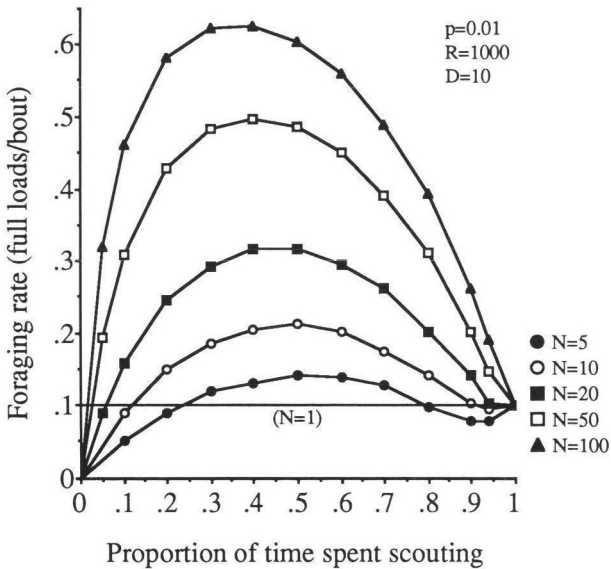


Fig. 8. Foraging rate vs proportion time spent scouting (s). Foraging rate is enhanced for a certain range of time spent scouting for each neighborhood size (N) (compare optimal values with those specified by search alone - Fig. 4). (In this sample series of curves, $p = 0.01$, $R = 1000$ and $D = 10$; collection is time-limited.)

Likewise, an individual in an IC population following a specific hybrid search strategy (fixed s) will be partly buffered against perturbations in environmental factors that shift the optimal value of s .

The effect of neighborhood size (N), predictability (p), and mean patch richness or duration (R, D) highlights the importance of understanding the several parameters that contribute to the value of s . SEELEY (1985b), for instance, reviewed various observations of the percentage of honeybee foragers specializing as scouts, with values ranging from 5-36%; but there is little supplemental data to evaluate these figures (though he notes that scouting increased when there was little forage; p. 84). BROWN (1986), likewise, has sought to quantify the behavior of cliff swallows, recording colony size, timing (absolute) patch-duration, and noting that 30-60% of the forays (mean \cong 40%) are based on following other foragers. The discussion of the information-center model above should clarify the set of measurements (s, N, p, R and D) needed for analysis and comparison of solitary versus IC foraging based on foraging rate.

5. Further considerations.

Several avenues of further investigation suggest themselves. The significance of the ephemerality of patches suggests that controlled experiments can be done - say, with honeybee hives - to explore the existence and nature of critical patch-duration. Second, the simulation itself may be developed, adding layers of variation or heterogeneity in each of the parameters (*e.g.* effects of crowding, "local enhancement" in collecting, or variation in scouting time among different foragers). In particular, information-centers have been associated with the ability to respond to differential patch quality and to switch foraging to a more profitable patch ("switching" has been noted in honeybees: LINDUAER, 1971; SEELEY, 1985a, 1985b; weaverbirds: DE GROOT, 1980; and great blue herons: KREBS, 1974). The proportion of time spent scouting, based on the general predictability of food in the environment, and group size, may all have some role in whether and how quickly switching occurs. Finally, in working beyond this study, one may explore how alternative search and recruitment strategies extend or modify the conclusions above.

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Résumé

Je présente un modèle mathématique et une simulation de fourrager avec un centre des renseignements (WARD & ZAHAVI, 1983). Les conditions les plus importantes pour un centre des renseignements seraient des limites de temps et des pièces de fourrager qui supportent biens des fourrageurs. L'échange des renseignements à un lieu central augmentait le degré de fourrager même si la probabilité de trouver le vivre serait haut (et non pas seulement quand des proies ou des pièces de fourrager seraient irrégulières). Des avantages d'un centre des renseignements seraient la plus fort pour des populations petites ($N < 20$), mais ils se agrandissaient en marge avec le nombre d'organismes. On peut détermine le temps critique pour la durée de la pièce et aussi le distribution optimal pour diviser le temps entre la reconnaissance et le recrutement. Une organisme ferait la reconnaissance presque la moitié du temps comme le vivre devrait irrégulier.