

# Integrating the Roles of Information and Competitive Ability on the Spatial Distribution of Social Foragers

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**ABSTRACT:** Understanding and predicting the spatial distribution of social foragers among patchily distributed resources is a problem that has been addressed with numerous approaches over the 30 yr since the ideal free distribution (IFD) was first introduced. The two main approaches involve perceptual constraints and unequal competitors. Here we present a model of social foragers choosing among resource patches. Each forager makes a probabilistic choice on the basis of the information acquired through past foraging experiences. Food acquisition is determined by the forager's competitive ability. This model predicts that perceptual constraints have a greater influence on the spatial distribution of foragers than unequal competitive abilities but that competitive ability plays an important role in determining an individual's information state and behavior. Better competitors have access to more information; consequently, we find that competitive abilities and perceptual constraints are integrated through the social environment occupied by individual foragers. Relative competitive abilities influence the forager's information state, and the ability to use information determines the resulting spatial distribution.

*Keywords:* assessment uncertainty, Bayesian assessment, habitat selection, ideal free distribution (IFD), perceptual constraints, unequal competitors.

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Explaining and predicting the distribution of organisms is a central objective in ecology. The choice of habitat by individuals will determine the distribution of organisms in the environment. When animals forage on patchily distributed resources, we can expect both the distribution of

resources and the distribution of competitors to affect foraging decisions.

Fretwell and Lucas (1970) proposed the ideal free distribution (IFD) to explain the distribution of organisms in patchy environments. The IFD predicts that, when there is a continuous input of resources, the distribution of organisms should match the distribution of resources. This prediction can be shown to follow from the basic assumptions that animals are perfectly informed about the distribution of resources (i.e., they are ideal), they can move about their environment without costs (i.e., they are free), all animals are equal competitors, and animals behave to maximize their intake rate. While these assumptions are rarely, if ever, met, the IFD can often predict the distribution of animals (Milinski 1988; Milinski and Parker 1991), though not always (Kennedy and Gray 1993; Tregenza 1995).

Even when animals approximate the distribution of resources, they tend to consistently undermatch the resource distribution, that is, underuse the good patch and overuse the poor patch (Abrahams 1986; Kennedy and Gray 1993). To explain this bias, researchers have relaxed the assumption of either equal competitors or ideal knowledge, providing a rich literature on IFDs with unequal competitors (e.g., Parker 1982; Sutherland 1983; Parker and Sutherland 1986; Houston and McNamara 1988; Hügler and Grand 1998; Ruxton and Humphries 1999) or perceptual constraints (e.g., Abrahams 1986; Gray and Kennedy 1994; Spencer et al. 1995, 1996; Ranta et al. 1999). When the assumption of ideal knowledge is relaxed, it is typically assumed that animals have a limit on perceivable mean differences, as per Abrahams's (1986) perceptual limits model (cf. Kennedy and Gray 1993; Spencer et al. 1995, 1996; Cartar and Abrahams 1997). However, this approach assumes that, even though animals have a perceptual limit, resource patches are immediately and accurately recognized. As Gray and Kennedy (1994) discovered, perceptual limits must change to explain increased deviations from the IFD as the rate of food input is decreased (as would be expected from Weber's Law). An alternative approach to relaxing the assumption of ideal knowledge is to assume

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that foragers are uninformed and must learn the resource distribution. This approach (see Tregenza 1995 for a review) has spawned learning rules, such as the relative payoff sum (Harley 1981) and its application to the IFD (Milinski 1984; Regelman 1984) and Ollason's (1980) threshold rule and its application to the IFD (Ollason 1987; Ollason and Yearsley 2001). Recent theoretical work suggests that learning rules can resist invasion from competing learning rules only under limited conditions; that is, they generally do not represent an evolutionarily stable strategy (Beauchamp 2000). Luttbeg's (2002) comparison of learning rules suggests that a comparative Bayes rule tends to outperform best-of- $n$  and threshold rules under most conditions. Koops (1998) provides an approach that combines the perceptual constraints and patch assessment approaches in a manner similar to the comparative Bayes rule explored by Luttbeg (2002). Foragers begin without information. Information, acquired by sampling patches, is used to form assessments of patch quality with uncertainty via Bayesian updating. The patch choice decision is made on the basis of the probability of choosing the best patch—that is, the patch that maximizes personal acquisition rates—and perception is constrained by the assessment uncertainty, not a predefined limit.

The equal competitor assumption is relaxed by allowing foragers to differ in their ability to acquire food. This has been accomplished by assuming that there are two classes of forager (good and poor) or by assuming that competitive ability varies continuously (Tregenza 1995). In either case, the same general conclusion is reached: forager numbers undermatch the distribution of food, but competitive units (the sum of all competitive abilities in a patch) match the distribution of food. This occurs because, even though foragers differ in their competitive ability, they are still perfectly informed.

While the unequal competitors and perceptual constraint approaches have been pursued separately and often at odds (are deviations due to unequal competitive abilities or a perceptual constraint?), it is likely that competitors are both unequal and imperfectly informed. Our objective is to integrate the unequal competitor and perceptual constraint approaches by developing a model where foragers are competitively unequal and imperfectly informed. Competitors are made unequal by assuming that competitive ability varies continuously, and perception is constrained by uncertainty in the assessment of patch quality. We then use this model of unequal, imperfectly informed social foragers to investigate the factors affecting their spatial distribution. To validate our model results (Rykiel 1996), we first show how imperfect information affects spatial distributions and then how unequal competitive abilities affect spatial distributions. Finally, we ask whether

we can understand the spatial distribution of social foragers as arising from a common mechanism.

### The Model

To model the patch-selection decisions of imperfectly informed foragers with unequal competitive abilities, we used an individual-based modeling (IBM) approach (DeAngelis and Gross 1992). For an IBM, the behavior of each individual within the computer simulation is coded and controlled individually. The resulting spatial distribution of the group becomes an emergent property of how individuals make patch-choice decisions. Since we are modeling the patch-selection behavior of social foragers, we will compare the spatial distribution results of this model with the Nash equilibrium—that is, the IFD—to determine how imperfect information and competitive inequalities influence the ability of social foragers to optimize their behavior. We focus on a continuous-input two-patch system, since this is consistent with and makes our model results comparable to most experimental tests of the IFD (Kennedy and Gray 1993; Cartar and Abrahams 1997) and much of IFD theory. In cases where three or more patches have been explored, the results are consistent with the two-patch system (e.g., Moody and Houston 1995; Ollason and Yearsley 2001). However, when testing the IFD with more than two patches, care must be taken not to falsely accept the hypothesis of the IFD (Cartar and Abrahams 1997). We have chosen to model the simplest system that allows us to examine the links between unequal competitor and perceptual constraint approaches. There are many complications that have been added to the IFD (for reviews, see Tregenza 1995; Giraldeau and Caraco 2000), including interference competition (Sutherland 1983), travel costs (Korona 1990; Åström 1994; Kennedy and Gray 1997), resource dynamics (Lessells 1995), predation risk (Giske et al. 1997), and spatially explicit resource dynamics (Stephens and Stevens 2001; Kshatriya and Cosner 2002). These are all worthy complications to be added once a simpler approach has been explored.

In our continuous-input two-patch system, food enters patches at a set rate according to a Poisson process. Food is distributed with  $R$  proportion entering patch A and  $1 - R$  proportion entering patch B. As foragers search for food, they use personal sample information to estimate patch quality. This estimate is based on the number of food items encountered,  $r$ , and the amount of time,  $t$ , to encounter those food items (Pratt et al. 1995). Our modeled foragers use a Bayesian assessment approach, where a prior expectation of patch quality is updated on the basis of current information to form a posterior expectation of patch quality. This posterior expectation can then be used as the prior expectation to form future assessments. A

Poisson process can be updated according to the following rules (Mangel 1990):

$$\begin{aligned} r_i'' &= \psi r_i' + r_i + (1 - \psi)r_0, \\ t_i'' &= \psi t_i' + t_i + (1 - \psi)t_0. \end{aligned} \tag{1}$$

The prior expectation of reward ( $r$ ) and time ( $t$ ) are denoted with a prime ( $'$ ); the posterior, or updated, expectation by a double prime ( $''$ ); and the current values with no prime. The variables  $r_0$  and  $t_0$  represent the default values for  $r$  and  $t$ , respectively;  $\psi$  is the rate at which prior information is devalued, which we will call memory. A  $\psi$  value of 0 represents no memory, and 1 represents perfect memory. When a forager does not sample a patch, assessments are updated with  $r_i = t_i = 0$ . When a patch is not sampled, the assessments of  $r_i''$  and  $t_i''$  decay toward  $r_0$  and  $t_0$  at a rate dependent on  $\psi$ . When a forager does sample a patch,  $r_i$  is the number of food items encountered, and  $r_i''$  is a weighted assessment of the number of food items acquired in patch  $i$ . For each time step spent in a patch,  $t_i = 1$  and  $t_i''$  is a weighted assessment of the number of time steps spent foraging in patch  $i$ . These updating rules assume that all time steps are equal (Mangel 1990).

The expected rate of encounter in a patch (DeGroot 1970; Mangel 1990) is

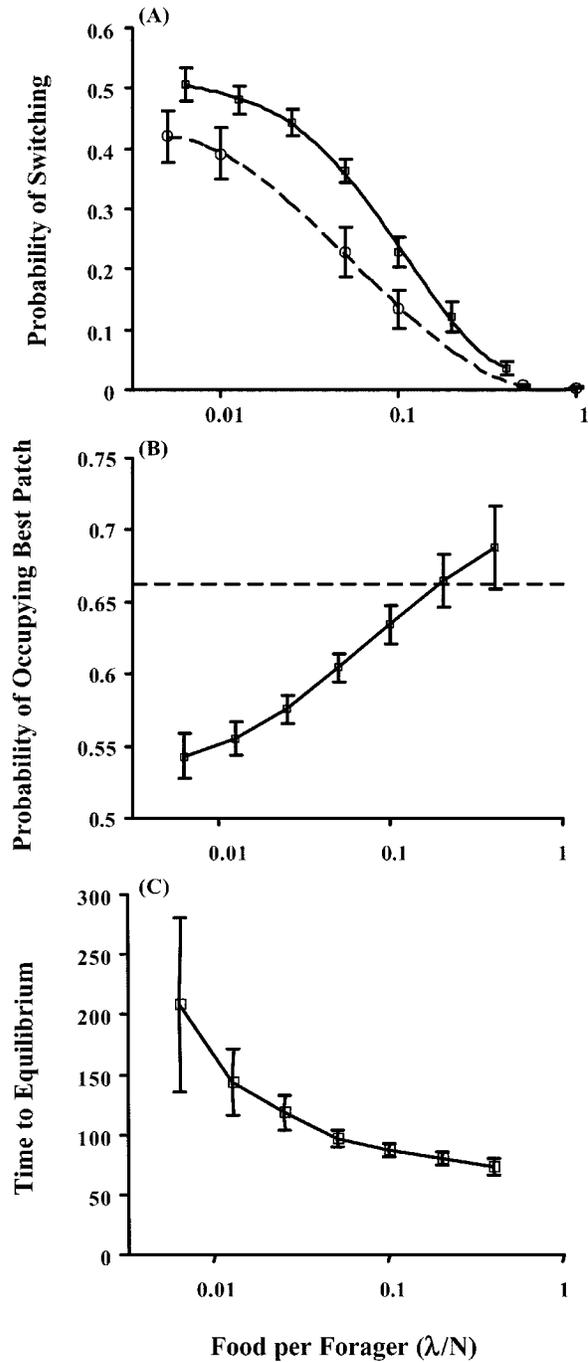
$$\bar{\lambda}_i = \frac{r_i''}{t_i''}. \tag{2}$$

Uncertainty about the assessed rate of encounter (DeGroot 1970; Mangel 1990) is

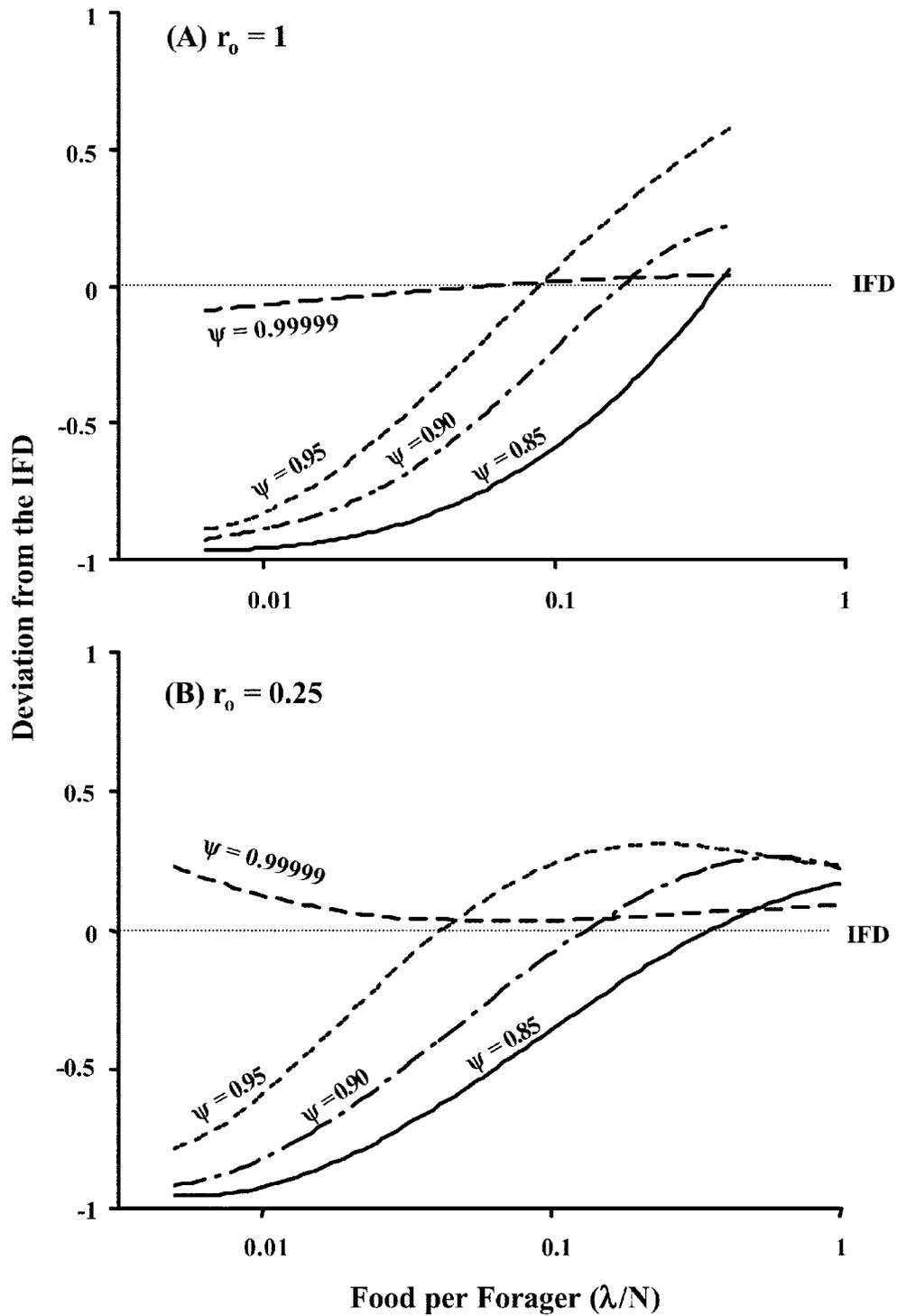
$$s_i^2 = \frac{r_i''}{t_i''^2}. \tag{3}$$

An imperfectly informed forager need only remember  $r_i''$  and  $t_i''$  to maintain a current assessment of patch quality and the uncertainty about that assessment.

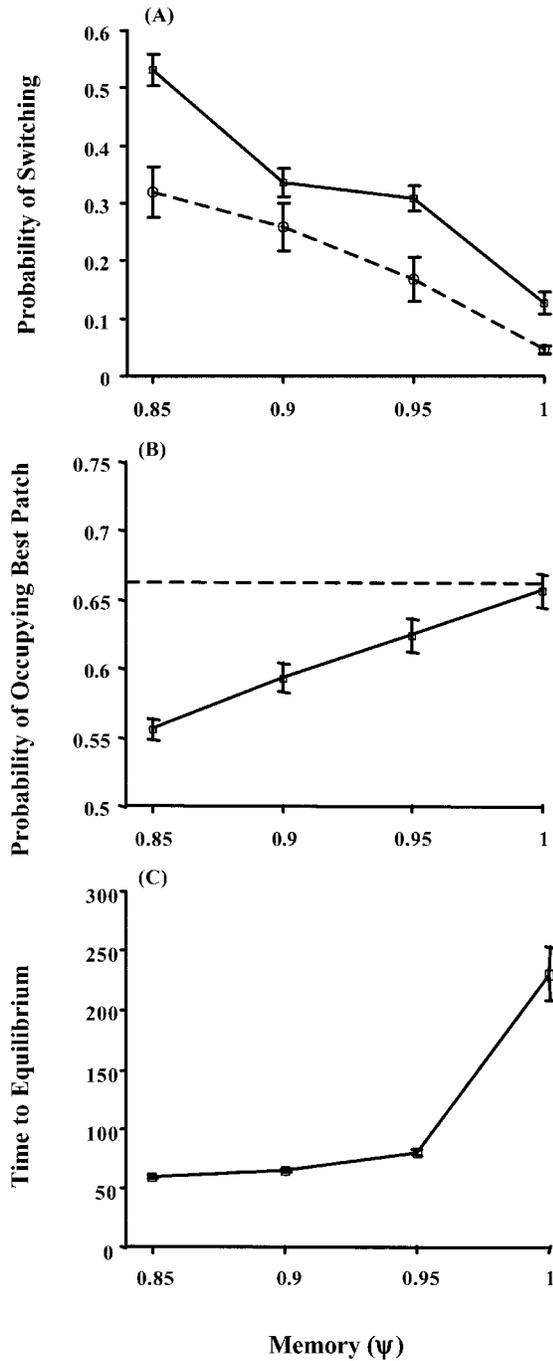
To seed the simulations, we gave all foragers a prior expectation of  $r_0 = 1$  and  $t_0 = 1$  so that  $\bar{\lambda}_i = 1$  and  $s_i^2 = 1$  for each patch, with a default assessment that all patches are equal. Since the initial prior expectation is based on only one time step of information, its effect on patch assessment will be quickly swamped by current information. Manipulation of the default expectation showed that much of the model output is not affected by  $r_0$ , with the exception of the probability of switching and conformity to the IFD. While  $r_0$  does influence switching and conformity to the IFD, the patterns examined in the model results are unaffected (figs. 1A, 2, 3A); therefore, we report the model results on the basis of the default expectation of  $r_0 = 1$ .



**Figure 1:** Influence of food per forager ( $\lambda/N$ ) on (A) the probability of switching patches (solid line represents the base model; dashed line represents a subset of simulations with  $r_0 = 0.25$ ,  $N = 10$ , and  $\lambda = \{0.05, 0.10, 0.50, 1, 5, 10\}$ ); (B) the probability of occupying the best patch (reference line represents the IFD), and (C) the time to equilibrium ( $t_{eq}$ ) of competitive units (similar patterns were observed in  $t_{eq}$  of forager numbers). Error bars represent 1 SE. Unless otherwise stated, parameter values as per table 1.



**Figure 2:** Deviation from the IFD-predicted distribution of forager numbers as a function of food per forager ( $\lambda/N$ ) for the four values of memory ( $\psi$ ). *A*, Results from the base model with parameter values as per table 1. *B*, Results from a subset of simulations with  $r_0 = 0.25$ ,  $N = 10$ , and  $\lambda = \{0.05, 0.10, 0.50, 1, 5, 10\}$  (other parameter values as per table 1). *Dashed line*,  $\psi = 0.99999$ ; *dotted line*,  $\psi = 0.95$ ; *dashed-dotted line*,  $\psi = 0.90$ ; *solid line*,  $\psi = 0.85$ . Reference line indicates conformity to the IFD. Positive deviations represent overmatching; negative deviations represent undermatching. Similar deviations were observed in the distribution of competitive units.



**Figure 3:** Influence of memory ( $\psi$ ) on (A) the probability of switching patches (solid line represents the base model; dashed line represents a subset of simulations with  $r_0 = 0.25$ ,  $N = 10$ , and  $\lambda = \{0.05, 0.10, 0.50, 1, 5, 10\}$ ), (B) the probability of occupying the best patch (reference line represents the IFD), and (C) the time to equilibrium ( $t_{eq}$ ) of competitive units (similar patterns were observed in  $t_{eq}$  of forager numbers). Error bars represent 1 SE. Unless otherwise stated, parameter values as per table 1.

Modeled foragers estimate the best patch using the  $Z$  model of perceptual constraints as the decision rule (Koops 1998). This assumes that foragers have been selected to maximize personal food intake rate and that travel time and costs are negligible (as per Fretwell and Lucas 1970). The decision rule is stochastic, and modeled foragers choose to forage in patch A with probability  $P(\bar{\lambda}_A > \bar{\lambda}_B)$  and choose patch B with probability  $1 - P(\bar{\lambda}_A > \bar{\lambda}_B)$  on the basis of the draw of a random number. The probability that patch A is better than patch B is based on the area under a normal distribution (e.g., DeGroot 1970; Pratt et al. 1995) and is defined as

$$P(\bar{\lambda}_A > \bar{\lambda}_B) = \Phi(Z) = \int_{-\infty}^Z \frac{1}{\sqrt{2\pi}} e^{-x^2/2} dx, \quad (4)$$

where

$$Z = \frac{\bar{\lambda}_A - \bar{\lambda}_B}{\bar{s}} \quad (5)$$

and

$$\bar{s} = \sqrt{\frac{s_A^2}{v_A} + \frac{s_B^2}{v_B}}. \quad (6)$$

The variable  $v_i$  is the weighted number of samples taken from each patch. In our model, the weighted number of samples is equivalent to the weighted number of time steps spent foraging in a patch so that  $v_i = t_i''$ ;  $\Phi(Z)$  is a monotonically increasing function over the range of  $Z$ , and anything that increases the absolute value of  $Z$  will increase the perceptual ability of the forager (Koops 1998). Our use of the normal distribution to define  $\Phi(Z)$  is not necessarily the only possible approach. The critical feature of a  $\Phi(Z)$  function is that it monotonically increases on  $Z$ . We used this formulation because it makes explicit use of the forager's uncertainty about patch quality. Koops (1998) has shown that a  $\Phi(Z)$  function can be defined so that the  $Z$  model of perceptual constraints functions exactly like Abrahams's (1986) perceptual limits model.

All foragers are assigned a fixed competitive ability that determines their relative ability to acquire food in a patch. Each forager obtains a portion of food according to the proportion of competitive units it represents in the patch; that is, food is infinitely divisible. The assigned competitive ability,  $c_j$ , is a random value greater than 0 from a normal distribution with  $\mu = 1$  and  $\sigma = 0.25$ , using the Box-Mueller algorithm (Hilborn and Mangel 1997):

$$c_j = \mu + \sigma(\sqrt{-2 \log w_1}) \cos(2\pi w_2). \quad (7)$$

All  $w_i$  are uniform random numbers from the range 0 to 1.

To start each simulation ( $t = 0$ ), foragers are randomly distributed among patches. Every time step, all foragers simultaneously acquire food on the basis of their relative competitive ability, reevaluate their assessment and assessment uncertainty of the quality of each patch according to the updating rules (eqq. [1]–[3]), and then choose a new patch according to the decision rule (eq. [4]). Every forager chooses patches on the basis of their own independent assessment of patch quality.

### Model Output

Simulations were run for a total of 2,000 time steps ( $T_s$ ) for each of five food ratios ( $R$ ), four group sizes ( $N$ ), four total food input rates ( $\lambda$ ), and four memory values ( $\psi$ ; see table 1). Thus, we have data from 320  $R$ - $N$ - $\lambda$ - $\psi$  combinations, providing the slope of 64 group distribution versus food distribution regressions for each  $N$ - $\lambda$ - $\psi$  combination. Each parameter combination was replicated 500 times, and the mean proportion of forager numbers and the mean proportion of competitive units in patch A were recorded every six time steps (a sampling period) to generate group-level dynamics of the mean of 500 replicates for each  $N$ - $\lambda$ - $\psi$  combination. Each replicate was started with  $N$  foragers that were each randomly assigned a competitive ability (according to eq. [7]) and then randomly assigned to start in one of the two patches. All foragers started with the expectation that patches are equal, on the basis of  $r_0$  and  $t_0$ .

The equilibrium proportion of forager numbers (or competitive units) is based on the final 10% of the sampling periods. Starting at  $t = 1,800$ , the final 34 sampling periods are used to calculate the mean proportion of forager numbers (or competitive units) in patch A. Equilib-

rium is reached when the proportion in patch A settles at this mean  $\pm 0.02$  (the tolerance zone). Starting from  $t = 0$  (the start of the simulation), each sampling period is classified as being inside ( $p_t = 1$ ) or outside ( $p_t = 0$ ) the tolerance zone. Ten consecutive sampling periods are used to calculate the mean number of sampling periods when the group distribution is within the tolerance zone ( $\bar{p} = \sum_{i=1}^{t+9} p_i/10$ ). The time to equilibrium ( $t_{eq}$ ) is reached when  $\bar{p} \geq 0.9$ , as long as  $\bar{p}$  does not fall below 0.7 thereafter. These criteria, while arbitrary, ensure that  $t_{eq}$  is not established too soon and that equilibrium is not lost when a forager samples.

To measure conformity to the IFD, we calculate the slope of the log equilibrium proportion of forager numbers (or competitive units) in patch A,  $\log(n_A/N)$ , against the log proportion of food in patch A,  $\log R$ , for all 64  $N$ - $\lambda$ - $\psi$  parameter combinations. This analysis is similar to producing a version of figure 4 with a line for each  $N$ - $\lambda$ - $\psi$  parameter combination, the slope of which is our measure of conformity to the IFD. Deviation from the IFD is this slope minus 1 (the IFD-predicted slope). Negative deviations represent undermatching; positive deviations represent overmatching.

For the first 400 replicates of each parameter combination, data for each individual in each replicate were recorded, including competitive ability, the probability of switching (each time step), and the probability of occupying the better patch (each time step). To measure the influence of competitive ability on individual behavior, we regress the probability of switching and the probability of occupying the best patch against competitive ability for each parameter combination. The slopes are our measures of the influence of competitive ability on individual behavior.

Table 1: Model variables/parameters, values, and descriptions

Variable/parameter	Value	Description
$r'$ , $r''$	...	Prior and posterior assessment of $r$
$t'$ , $t''$	...	Prior and posterior assessment of $t$
$r$	...	Food items obtained in latest time step
$t$	0, 1	Occurrence of latest time step
$r_0$ , $t_0$	1, 1	Default assessment of $r$ and $t$
$T_s$	2,000	Number of time steps per model run
$R$	.20, .40, .50, .665, .75	Proportion of food in patch A
$\psi$	.85, .90, .95, .99999	Memory decay parameter
$\lambda$	.25, .50, 1.00, 2.00	Total rate of food input
$N$	5, 10, 20, 40	Total number of foragers
$\lambda/N$	.00625, .0125, .025, .05, .10, .20, .40	Total rate of food input per forager
$c_j$	...	Randomly assigned competitive ability
$\sigma$	.25	Standard deviation of distribution of $c_j$

### Data Analysis

To determine the relative influence of each model parameter, we use a forward stepwise multiple regression approach (Kleinbaum et al. 1988). Parameters or interactions that explained the most variance in the model results are included, allowing us to drop parameters and interactions that are not necessary to explain the model results. The criterion for inclusion in the regression model is a  $P$  value  $>.05$ , and any parameter is subsequently dropped from the regression model if its  $P$  value exceeds  $.10$ . We only report on the parameters and interactions the stepwise approach considers important for the explanation of the model results.

### Model Results

We present the model's results in four sections. First, we consider the amount of food entering the system per forager ( $\lambda/N$ ). In this model, foragers make decisions on the basis of the information they acquire from personal experience; thus, current information is the amount of food a forager acquires. By looking at the influence of food per forager on the behavior of individuals and the group, we can look at how information affects the spatial distribution of social foragers. Second, we consider the influence of memory ( $\psi$ ). Memory determines the weighting of past food discoveries and is the prior information available to foragers. By looking at the influence of memory on the behavior of individuals and the group, we can again look at how information affects the spatial distribution of social foragers. Third, we examine the influence of competitive abilities on the spatial distribution of social foragers by manipulating the variance in competitive abilities ( $\sigma$ ). Finally, to determine whether there is a commonality between imperfect information and unequal competitive abilities that acts as the integrative mechanism for determining the spatial distribution of social foragers, we look at how information and competitive ability interact to influence the spatial distribution of social foragers.

#### *Food per Forager: Current Information*

To acquire current information about the quality of patches, foragers must switch to sample alternative habitats. The average probability of switching is  $0.33$  ( $SD = 0.22$ ), ranging from a minimum of  $0$  to a maximum of  $0.63$ . As the availability of current information increases through increased food per forager ( $\lambda/N$ ), the probability of switching declines (fig. 1A). The probability that a forager occupies the best patch is also influenced by food per forager, increasing with  $\lambda/N$  (fig. 1B).

The time to reach equilibrium ( $t_{eq}$ ) was significantly

longer (paired  $t = 2.43$ ,  $df = 319$ ,  $P = .016$ ) for the distribution of competitive units ( $\bar{X} = 108.5$ ,  $SD = 122.68$ ) than for the distribution of forager numbers ( $\bar{X} = 102.2$ ,  $SD = 106.44$ ). Though the mean difference is small (6.3 time steps), this effect is consistent across most parameter combinations, with forager number  $t_{eq}$  longer than competitive unit  $t_{eq}$  in only 27 of 320  $R-N-\lambda-\psi$  combinations (binomial test,  $P < .001$ ). For this reason, we focus on time to equilibrium of competitive units, though the same pattern is observed in forager number  $t_{eq}$ . The time to reach equilibrium ranged from 73.7 time steps ( $SD = 33.53$ ) when  $\lambda/N = 0.40$  to an average of 208.2 time steps ( $SD = 322.73$ ) when  $\lambda/N = 0.00625$  (fig. 1C). This trend of increasing  $t_{eq}$  with decreasing  $\lambda/N$  is true for the distribution of both forager numbers and competitive units. As expected, the less current information available to foragers, the longer it takes them to make a final decision.

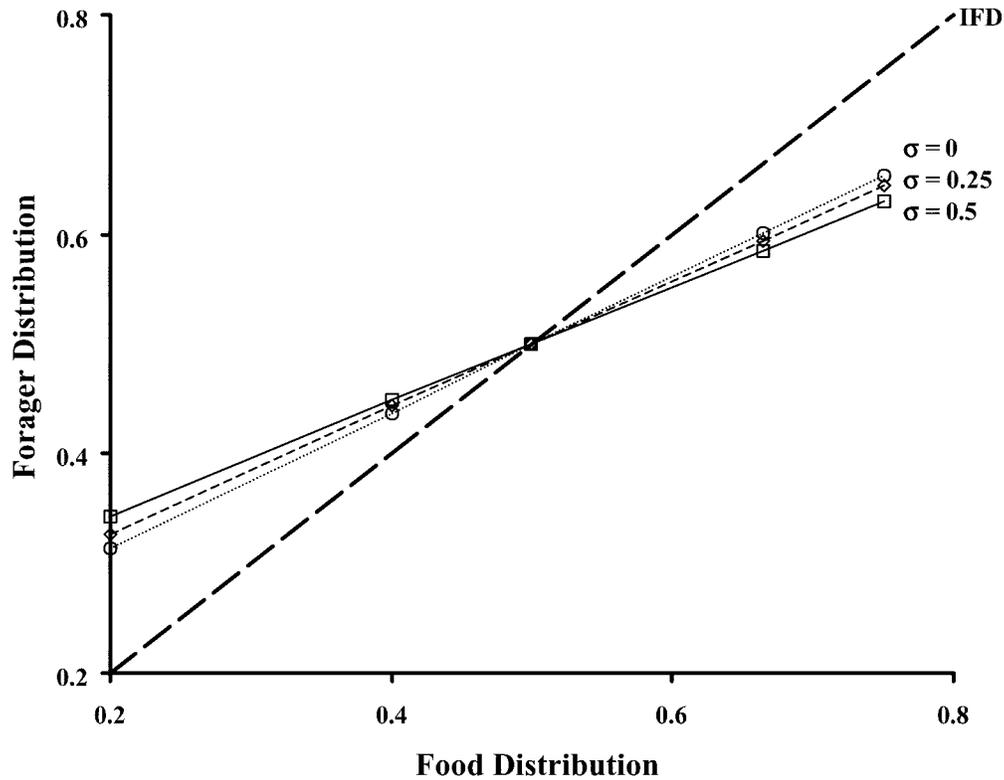
When food per forager, and hence current information, is limited, deviations from the IFD are greatest. The majority of forager distributions undermatch the distribution of resources, with slopes as low as  $0.03$ , that is, random patch selection at all food distributions (fig. 2). At low  $\lambda/N$  levels, undermatching is prevalent. As  $\lambda/N$  increases, the distribution of both forager numbers (fig. 2) and competitive units approaches the IFD. When  $\lambda/N$  is high, overmatching is common and is more likely to occur in the distribution of competitive units (table 2).

Food per forager ( $\lambda/N$ ), as the source of current information, eases habitat selection. Individually, foragers switch patches less frequently and are more likely to find the best patch. As a group, foragers conform more closely to the IFD and require less time to reach this equilibrium. These results are consistent with previous theoretical work on the influence of perceptual constraints on the IFD (Abrahams 1986). The perceptual limits model predicts that as forager numbers increase or food input decreases (either leading to lower  $\lambda/N$ ), conformity to the IFD decreases through increasing undermatching. Memory also constrains the information available to foragers; however, the influence of memory on spatial distributions has not been explored. We now consider the influence of memory.

#### *Memory: Prior Information*

When access to prior information is limited through reduced memory ( $\psi$ ), social foragers switch more often (fig. 3A). As memory increases, the probability that a forager occupies the best patch increases (fig. 3B). Time to equilibrium ( $t_{eq}$ ) increases gradually as memory increases from  $\psi = 0.85$  to  $0.95$  (fig. 3C). As memory is increased further to near perfect,  $t_{eq}$  jumps threefold with a maximum observed value of 1,026 time steps.

Undermatching the IFD decreases as forager memory



**Figure 4:** Proportion of forager numbers versus food in patch A for three of the four values of variance in competitive ability ( $\sigma$ ). Dotted line,  $\sigma = 0$ ; dashed line,  $\sigma = 0.25$ ; solid line,  $\sigma = 0.5$ . Presented data are only for simulations with  $N = \{10, 20\}$ ,  $\lambda = \{0.50, 1.00\}$ , and  $\psi = \{0.90, 0.95\}$ . The 1 : 1 reference line is predicted by the IFD. Data for  $\sigma = 0.1$  were omitted since they were indistinguishable from  $\sigma = 0$ . Other parameter values as per table 1.

increases, with near perfect memory ( $\psi = 0.99999$ ) providing excellent conformity to the IFD even when  $\lambda/N$  is limited (fig. 2A). This effect of memory is observed in both the distribution of forager numbers and competitive units.

Memory, as the source of prior information, eases habitat selection. When foragers have better memory, they switch patches less frequently and are more likely to find the best patch. As a group, conformity to the IFD improves, but it takes longer to reach equilibrium. The time to equilibrium results demonstrate that the cost of memory is slower adaptation to changing conditions. Even though the physical environment ( $\lambda$ ,  $N$ , and  $R$ ) does not change during these simulations, the social environment does as individuals choose to switch patches. As individuals move around, the profitability of each patch changes, and we see that when social foragers have a higher memory, they are slower to adapt to this change.

#### Role of Unequal Competitive Abilities

To examine the influence of competitive abilities on the spatial distribution of social foragers, we manipulated the variance in competitive abilities ( $\sigma$ ) to compare between equal competitors and unequal competitors. When  $\sigma = 0$ , competitors are equal (all  $c_i = 1$ ); when  $\sigma = 0.1$ , competitive abilities range from 0.4 to 1.6; and when  $\sigma = 0.25$  and 0.5, competitive abilities range from  $>0$  to 2.5 and 4, respectively. In each case, the mean competitive ability was constant at 1. We found that conformity of the group to the IFD was mildly influenced by variance in competitive ability (fig. 4). Variance in competitive ability decreased the ability of forager numbers to conform to the IFD (fig. 4); however, the ability of foragers to match their competitive units to the IFD increased. Thus, the conformity of forager numbers to the IFD was slightly worse when  $\sigma = 0.5$  than when competitors were equal ( $\sigma = 0$ ), but the conformity of competitive units was

**Table 2:** Comparison of slopes between the proportion of forager numbers or competitive units and the proportion of food

Competitive units:	Forager Numbers	
	Undermatch	Overmatch
Undermatch	$m_f = .37 (.25)$ $m_c = .42 (.29)$ $t = 5.57, df = 37, P < .001$	Not observed
Overmatch	$m_f = .94 (.029)$ $m_c = 1.08 (.061)$ $t = .72, df = 37, P = .49$	$m_f = 1.17 (.17)$ $m_c = 1.36 (.16)$ $t = 22.99, df = 37, P < .001$

Note: These analyses are divided into situations where forager numbers and competitive units undermatch or overmatch the resource distribution;  $m_f$  and  $m_c$  are the slopes of forager numbers and competitive units, respectively. Parenthetical values are standard deviations. All  $t$ -tests are paired. Note that in every case,  $m_f < m_c$ , so that when both competitive units and forager numbers undermatch, competitive units exhibit closer conformity to the IFD and vice versa when both overmatch.

slightly better. Variance in competitive abilities had little influence on time to equilibrium, with forager number  $t_{eq}$  ranging from a low of 69.9 time steps (SD = 12.04 at  $\sigma = 0.10$ ) to a high of 78.2 time steps (SD = 38.23 at  $\sigma = 0.25$ ). Time to equilibrium distribution of competitive units was even less affected by variance in competitive abilities, with  $t_{eq}$  ranging from 70.8 time steps (SD = 13.33 at  $\sigma = 0.10$ ) to 73.4 time steps (SD = 24.13 at  $\sigma = 0$ ). Thus, variance in competitive ability ( $\sigma$ ), while influencing the spatial distribution of social foragers, has a much smaller effect than imperfect information and can probably be ignored for the purpose of predicting spatial distributions.

### Integration

As an individual's competitive ability increases, it is more likely to occupy the best patch. Competitive ability always has a positive influence on an individual's probability of occupying the best patch, and this influence increases with increasing  $\lambda/N$  (fig. 5A) and with increasing  $\psi$  (fig. 5B). The more limited the information (low  $\lambda/N$  or low  $\lambda$ ), the less likely that the best competitors will occupy the best patch.

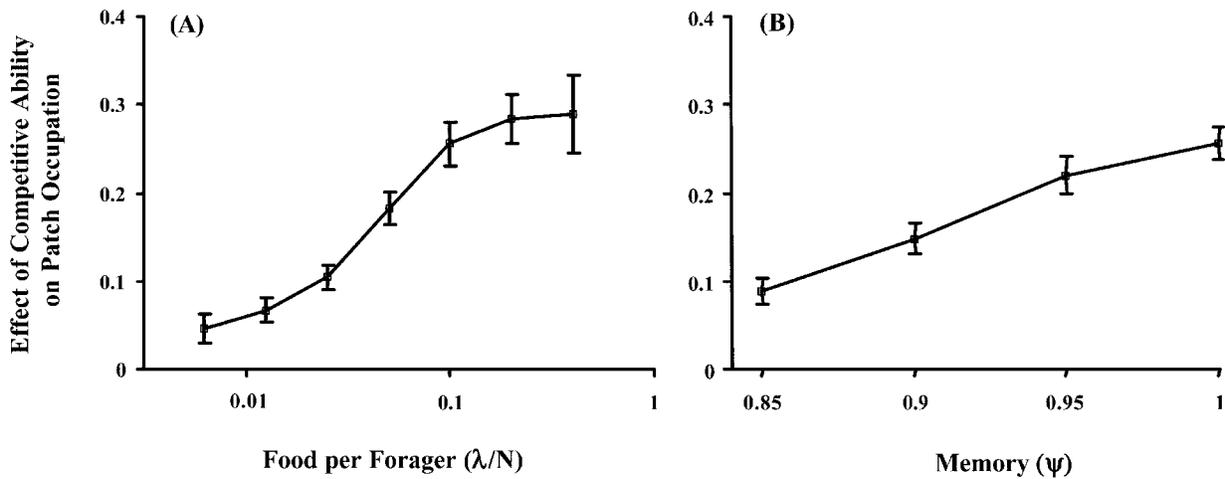
Increasing competitive ability generally decreases the probability of switching (fig. 6). The probability of switching and the influence that competitive ability has on switching are affected by both  $\lambda/N$  and  $\psi$ . When foragers are in a low information state where both current and prior information are limited, the probability of switching is high and competitive ability has little influence on switching (fig. 6A). When foragers are in a high information state where neither current nor prior information is limited, the probability of switching is low and, again, competitive ability has little influence (fig. 6D). At intermediate information states where either prior information

is limited (fig. 6B) or current information is limited (fig. 6C), the probability of switching is strongly influenced by competitive ability, with good competitors (high  $c_j$ ) switching less frequently than poor competitors (low  $c_j$ ). The mean slope of the relationship between switching and competitive ability is  $-0.13$  (SD = 0.13); however, the observed slopes range from  $-0.63$  to 0. The slope of this relationship is influenced by memory ( $\psi$ ) and food per forager ( $\lambda/N$ ), though not linearly (fig. 7). The influence of competitive ability on the probability of switching is greatest at intermediate levels of  $\lambda/N$ , though where this peak of influence occurs depends on  $\psi$ .

Competitive ability ( $c_j$ ) influences the forager's information state, increasing the ability of better competitors to perceive differences in patch quality. However, the advantage to greater competitive ability is dependent on the information state of competitors. When all foragers occupy a good information state (high  $\lambda/N$  or  $\psi$ ),  $c_j$  has little influence on switching but does allow the best competitors to find and occupy the best patch. As  $\lambda/N$  or  $\psi$  decreases,  $c_j$  confers an advantage because of improved information state. When information becomes scarce enough to limit the decisions of all competitors (low  $\lambda/N$  or  $\psi$ ), increased competitive ability provides no advantage, and the best competitors are no more likely to occupy the best patch than the worst competitors. Thus, the unequal competitors approach and the perceptual constraints approach have the same foundation in access to information. The more information available to a forager, the better its decisions, and higher competitive ability increases the information available to a forager by allowing the forager to acquire more food.

### Discussion

By combining unequal competitive abilities and imperfect information into a single model, we have shown that the



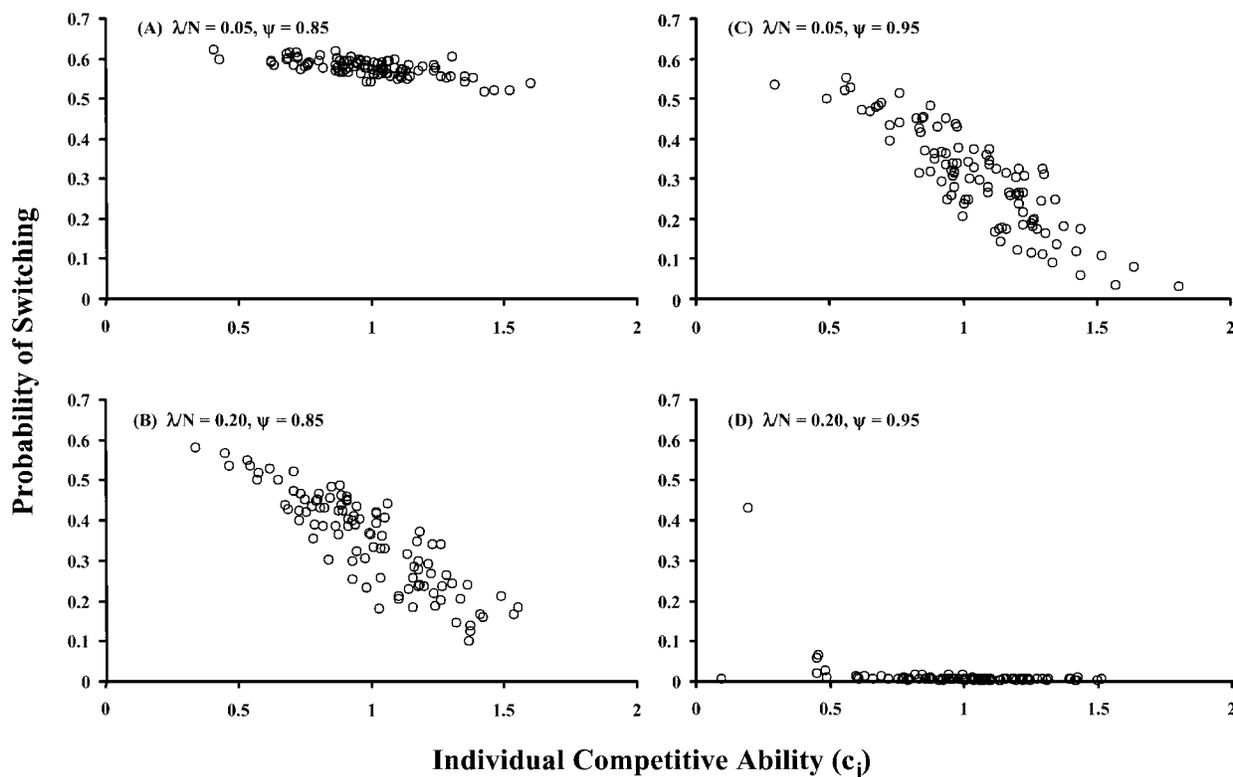
**Figure 5:** Influence of competitive ability ( $c_i$ ) on the probability of occupying the best patch, measured by the slope, as a function of (A) food per forager ( $\lambda/N$ ) and (B) memory ( $\psi$ ). Error bars represent 1 SE. Parameter values as per table 1.

impact of information on the spatial distribution of foragers is of greater import than competitive asymmetries. However, our model goes further by integrating the influence of imperfect information, in the form of assessment uncertainty, with the unequal competitors approach. In the perceptual constraints approach, deviations from the IFD are caused by imperfect information and the inability of foragers to perceive a difference in patch quality. Our model predicts that differences in competitive ability translate into differences in information state through access to information. Imperfect information and the differential ability of good and poor competitors to perceive differences in patch quality ultimately cause deviations from the IFD.

Our model's dynamics are driven by the ability of foragers to process information. From the simulation results, it is apparent that there are two parameters of importance in the processing of information: memory ( $\psi$ ) and food per forager ( $\lambda/N$ ). Memory determines how much prior information is included in the current assessment, and food per forager determines how much current information a forager can acquire. A forager acquires current information from two sources: food and time. Increased time spent foraging—that is, increased sample size—decreases assessment uncertainty leading to greater perceptual ability. Thus, a forager acquires information about the quality of a patch regardless of the amount of food acquired. However, food is an important source of information. The more food a forager acquires, the greater its assessed mean intake rate, and the greater its perceptual ability. Thus, it is the food available to a forager ( $\lambda/N$ ) that is important and not solely the total food input rate

( $\lambda$ ) or the number of competitors ( $N$ ). This effect is observed in a number of simulation results. When  $\lambda/N$  increases, we observe closer conformity to the resource distribution (fig. 2) and a decrease in the time for a group to reach equilibrium (fig. 1C). On an individual basis, increasing  $\lambda/N$  decreases switching (fig. 1A), increases recognition of the better patch (fig. 1B), and decreases the influence of competitive ability on switching (fig. 7). Furthermore, better competitors are better perceivers because they acquire more food. Acquiring more food provides more information and simplifies the discrimination problem. Consequently, unequal competitors occupy different information states. This is apparent through the influence of competitive ability on switching and occupation of the better patch. As competitive ability increases, switching declines (fig. 6), and the probability that the individual occupies the better patch increases.

Switching is determined by uncertainty in patch assessment. As uncertainty increases,  $Z$  is pushed toward 0 (i.e.,  $|Z| \rightarrow 0$ ), the probability that one patch is better than another decreases (i.e.,  $\Phi(Z) \rightarrow 0.5$ ), and the probability of switching patches increases. However, the influence of competitive ability on switching is not consistent. As  $\lambda/N$  decreases, competitive abilities play a greater role in switching (fig. 7). The poorer competitors drive this change. As  $\lambda/N$  decreases, fewer poor competitors obtain enough food to perceive a difference in patch quality, leading to greater undermatching and increased benefits to occupants of the better patch. As  $\lambda/N$  declines further, competitive abilities lose their influence on switching as differences in patch quality become imperceptible to the best competitors. This process, however, is mediated by



**Figure 6:** Probability of switching patches as a function of individual competitive ability ( $c_j$ ) for the first 100 foragers in a sample of simulations with (A)  $\lambda/N = 0.05$ ,  $\psi = 0.85$  (slope =  $-0.068$ ), (B)  $\lambda/N = 0.20$ ,  $\psi = 0.85$  (slope =  $-0.40$ ), (C)  $\lambda/N = 0.05$ ,  $\psi = 0.95$  (slope =  $-0.42$ ), and (D)  $\lambda/N = 0.20$ ,  $\psi = 0.95$  (slope =  $-0.063$ ). In each case,  $R = 0.2$ . Other parameter values as per table 1.

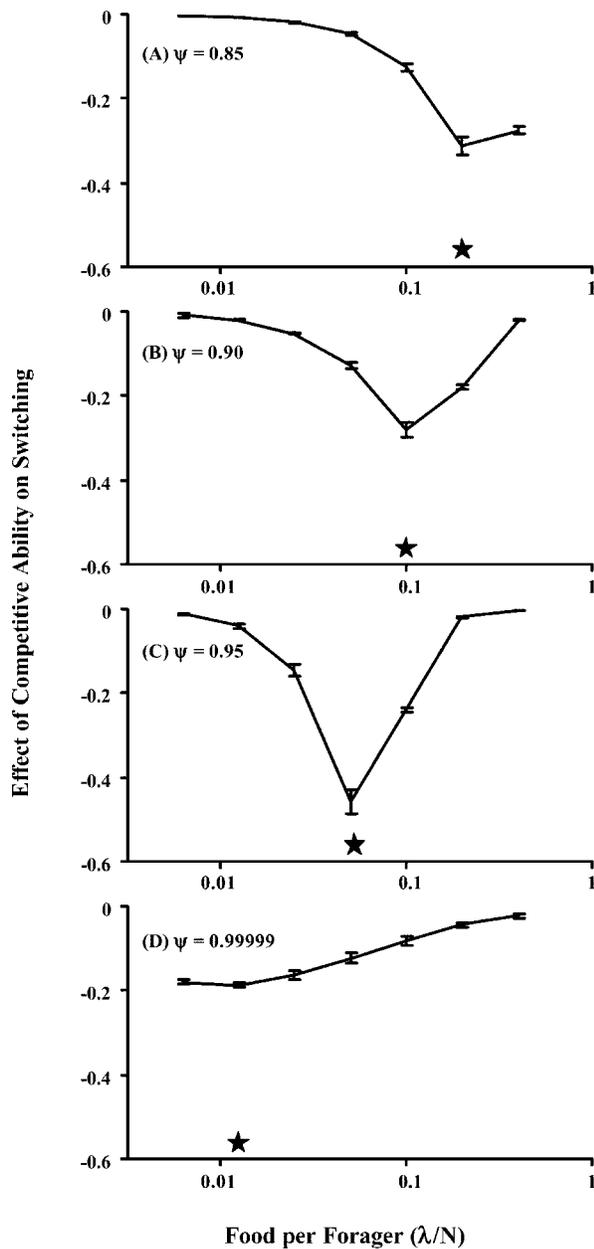
memory. Increasing memory increases access to prior information and changes a forager's information state. As the discrimination problem eases, the importance of competitive ability declines, and the point of maximal influence of competitive ability on switching shifts to lower  $\lambda/N$  levels (fig. 7). For the same reasons discussed for switching, we see a decline in the importance of competitive ability on foraging location as  $\lambda/N$  decreases (fig. 5). When  $\lambda/N$  is high, all foragers accurately determine the better patch, and the group exhibits closer conformity to the IFD (fig. 2). So why do better competitors still occupy the best patch? The answer is a matter of history. Even though foragers were not added sequentially (as per Abrahams 1986; Spencer et al. 1995, 1996; Houston and Lang 1998), history is still important (as per Spencer et al. 1995) because better competitors realize and occupy the best patch earlier, thereby decreasing its value to poorer competitors.

History can also explain the observed overmatching (fig. 2). With the exception of near-perfect memory, overmatching diminishes with lower memory and increases with food per forager. Most overmatching occurs at higher levels of  $\lambda/N$ , conditions where all foragers have access to

a good supply of current information. With foragers in a high information state, all foragers realize early which patch provides higher intake rates as a result of undermatching as the group distribution approaches the IFD from the initial random distribution. Early preference for the better patch among most group members results in overmatching, and higher memory values can be costly by trapping groups into these early assessments.

#### *Perceptual Constraints versus Unequal Competitors*

Deviations from the IFD have typically been explained as violations of the assumption of either equal competitors (Parker and Sutherland 1986) or ideal knowledge (Abrahams 1986). However, these explanations are not mutually exclusive. Houston and McNamara (1988) conclude by stating that the combined effects of unequal competitive abilities and perceptual constraints could be additive, producing greater undermatching. Spencer et al. (1995) published results of computer simulations of perceptually limited unequal competitors that showed this result, though their results may have been influenced by a programming



**Figure 7:** Influence of competitive ability ( $c_i$ ) on the probability of switching patches, measured by the slope (see fig. 6), as a function of food per forager ( $\lambda/N$ ) for (A)  $\psi = 0.85$ , (B)  $\psi = 0.90$ , (C)  $\psi = 0.95$ , and (D)  $\psi = 0.99999$ . Star on the abscissa marks where competitive ability maximally affects switching for each memory value. Note that the point of maximal effect shifts to lower  $\lambda/N$  as memory increases. Error bars represent 1 SE. Other parameter values as per table 1.

error (Houston and Lang 1998). When we removed unequal competitive abilities from our model ( $\sigma = 0$ ), we observed minimal changes in the distribution of foragers (fig. 4). This suggests that, as Hugie and Grand (1998)

concluded, “competitive inequalities, which are usually difficult to quantify, may often be safely ignored” (p. 17). Though this may be true if we are only interested in predicting the distribution of organisms among patches (as stated in Hugie and Grand 1998), ignoring competitive abilities ignores the system dynamics, such as the influence of competitive ability on switching behavior (Milinski 1984) and patch occupancy (Grand 1997; Tregenza and Thompson 1998). For example, our model predicts that better competitors should reside in the better quality patches without assuming that better competitors arrive first (Spencer et al. 1995), that competitive abilities vary across patches (Parker and Sutherland 1986), or that foragers arrive sequentially (Houston and Lang 1998). Instead, this result arises from differences in the information states occupied by unequal competitors.

Another difference between previous models and ours is the predicted distribution of competitive units. Models of unequal competitors (Parker and Sutherland 1986) predict that, while the distribution of forager numbers may undermatch, the distribution of competitive units will conform to the resource distribution. This is a result of assuming that foragers are perfectly informed; as Spencer et al. (1995) showed, when unequal competitors and perceptual constraints are combined, the distribution of competitive units will also deviate from the IFD. Spencer et al.’s (1995) model, however, only showed undermatching. Overmatching of foragers does occur (see review by Kennedy and Gray 1993), and our model predicts that the distribution of competitive units are more likely to overmatch (table 2), especially when the distribution of forager numbers conform well to the IFD or overmatch. Coho salmon, *Oncorhynchus kisutch*, appear to distribute themselves among patches according to their competitive units, exhibiting some undermatching (Grand 1997; Grand and Dill 1997). Measuring competitive abilities is not common, and overmatching of competitive units has not been observed.

### Testing the Model

Testing the influence of memory on conformity to an IFD may be difficult, especially if memory is subject to stabilizing selection. There are two immediately apparent approaches to testing model predictions about memory. The first is the approach of Mackney and Hughes (1995), who used groups from three different populations of sticklebacks to test for differences in memory. They found that residential marine sticklebacks had the shortest memory window (8 d,  $\psi = 0.875$ ), followed by anadromous sticklebacks (10 d,  $\psi = 0.90$ ) and residential freshwater sticklebacks (>25 d,  $\psi > 0.96$ ). Our model predicts that freshwater sticklebacks should exhibit closer conformity to the

IFD than marine sticklebacks, though it will take them longer to reach equilibrium. Similar comparisons can be made between species from stable environments where memory should be high and unstable environments that would select for lower memory. Alternatively, if memory is flexible to local foraging conditions, as observed in least chipmunks and golden-mantled ground squirrels (Devenport and Devenport 1994), groups of foragers could be held under predictable and unpredictable food conditions. Unpredictable conditions should select for lower memory than predictable conditions and produce greater deviations from an IFD. This contrasts with a fixed memory that is a population-specific character.

The rate of food input per forager is an easier way to test the model. As  $\lambda/N$  increases, conformity to an IFD increases, and time to reach equilibrium decreases. An increase from low to medium  $\lambda/N$  should increase the influence of competitive ability on switching behavior. As  $\lambda/N$  increases from medium to high, the influence of competitive ability will decrease. The rate of food input per forager can be manipulated by changing food input rates or group size. When changing group size, however, one must be careful of the effect of interference (Gillis and Kramer 1987), which was not included in this model. Increasing food input can also increase the rate of food input per forager. In the only experimental test of this prediction, Gray and Kennedy's (1994) mallard results are consistent with this prediction. Unfortunately, Gray and Kennedy (1994) did not report on the competitive abilities of their foragers or the effect that competitive ability had on patch occupation or switching behavior.

Finally, our model makes the unique prediction that the combined effects of information and variation in competitive abilities on the spatial distribution of social foragers will be nonadditive. This prediction can be tested experimentally using a two-way factorial design that manipulates information and variation in competitive abilities as the two main effects. Information can be manipulated environmentally. For visually foraging fish, one approach would be to run experiments in clear or turbid water (e.g., Abrahams and Kattenfeld 1997). Birds could be manipulated foraging in short or tall grass. Variation in competitive abilities could be achieved through size (e.g., Cutts et al. 1999), age (e.g., Smith and Metcalfe 1994), hormone (e.g., Johnsson and Björnsson 1994), or transgenic (e.g., Devlin et al. 1999) manipulations. The specific test of our hypothesis would be a significant interaction between these two main effects. Our model also predicts that manipulations affecting access to information should have a greater influence on the spatial distribution of foraging animals than increasing the variance in competitive abilities.

## Conclusions

Our model is similar to previous models of the IFD in that, while patch assessment is formed by Bayesian updating, the updating rules (eq. [1]) take a form similar to simple linear operator models (Mangel 1990). However, our model differs from previous models by combining the perceptual constraints and patch assessment approaches with the unequal competitors approach. We assume that individuals make decisions based on relative differences, that is, differences relative to assessment uncertainty (eq. [5]). Many of the dynamics that emerge from our model are consistent with both the predictions of previous models and experimental observations. However, our model performs better than previous models by incorporating dynamics predicted by both the perceptual constraints approach, such as the influence of food input rates (Gray and Kennedy 1994), and the unequal competitors approach, such as the influence of competitive ability on switching behavior (Milinski 1984) and patch occupancy (Grand 1997; Tregenza and Thompson 1998). As with the perceptual constraints and patch assessment approaches, we find that when information is limited, foragers switch patches more frequently and undermatch the resource distribution and that conformity to the IFD improves with increased access to information.

Unlike previous IFD models, our model demonstrates that an increased rate of food acquisition provides a more accurate source of information. Food per forager ( $\lambda/N$ ) provides a very testable way to manipulate current information. Increased memory also provides increased access to information, a source of information that has not been explored in previous IFD models or experiments. As with the unequal competitors approach, we find that patch occupancy and switching are correlated with individual competitive abilities and that increasing the variance in competitive abilities increases undermatching in forager numbers while improving conformity of competitive units to the IFD, though these effects are minimal. The minimal effect of competitive inequalities on the spatial distribution of foragers is unique to our model. Since most previous models have considered either unequal competitors or perceptual constraints, they have always predicted a significant effect of competitive inequalities, with the exception being Hugie and Grand (1998). Ours is the first model to predict the relative importance of factors that can influence deviations from the IFD (Tregenza 1995). Our model predicts that perceptual constraints and competitive inequalities will not be additive (unlike Houston and McNamara 1988; Spencer et al. 1995); rather, there will be an interaction with competitive ability playing an important role at intermediate levels of information.

We use our model to explore the interaction between

unequal competitors and perceptual constraints. Increasing competitive ability increases access to information, and we generally see a decrease in patch switching. Competitive inequalities affect group dynamics because of the effect that competitive abilities have on access to information. Better competitors have access to more information about patch quality because of their increased rate of food acquisition, and good and poor competitors occupy different information states. Information about patch quality is an important resource. Foragers with imperfect information are constrained to making suboptimal foraging decisions with the resulting negative consequences for fitness (Lemon and Barth 1992). Foragers with more information are able to take advantage of unexploited resources, such as the underuse of good foraging patches, with the resulting increase in foraging rate and fitness. Thus, our model demonstrates that the integration of unequal competitive abilities and perceptual constraints occurs through the social environment occupied by individual foragers. Relative competitive abilities generate information niches, and the ability to use information within that niche determines the spatial distribution of social foragers.

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