TR - H - 160

Simulating probability matching in groups of foraging animals: A comparison of representational and nonrepresentational models

James S. Magnuson

1995. 7. 25

Simulating probability matching in groups of foraging animals: A comparison of representational and nonrepresentational models

James S. Magnuson

ATR Human Information Processing Laboratories, 2-2 Hikaridai, Seika-cho, Soraku-gun, Kyoto, 619-02 Japan

Abstract

Representational approaches to animal behavior (e.g., [1, 5]) posit that complex group behavior results from complex representations of events within the central nervous systems of individual animals. I present the results of a simulation of foraging behavior in groups of organisms, in which simple behavioral rules at the individual level result in the emergence of "probability matching" to food sources, a complex group behavior observed in various species. The success of the simulation reaffirms the notion that representations of an environment can occur at the level of the group, and suggests that models of complex behaviors observed in groups should begin with the simplest possible rules at the individual level.

1 Introduction

Naturalists commonly observe "probability matching" among groups of various species. Presented with multiple sources of food in an environment, individuals quickly divide into groups proportionate to the density of food available from each source (see [1], chapter 11, for an overview). It is important to note that the overall density of food is what determines the size of the groups. Given two sources dispersing morsels of equivalent magnitudes at equivalent rates, the animals divide into two groups of approximately equal numbers clustered around each of the sources. If the amount of food available from one source increases, due to an increase in either its rate of dispersal or the magnitude of the morsels of food, the size of the groups of animals changes proportionately.

Gallistel [1] (among others, e.g., [5]) has explained such behavior as the result of very complex and specific representations of the food source characteristics in the central nervous systems of individual organisms:

> [Results suggest] that birds accurately represent rates, that they accurately represent morsel magnitudes, and that they can multiply the representation of morsels per unit time by the representation of morsel magnitude to compute the internal variables that determine the relative likelihood of their choosing one foraging patch over the other. (p. 358)

Are the complex mathematical abilities Gallistel and others describe truly crucial for the apparent rationality of, for example, ducks? Could animals instead follow simple rules, with the result that the probability of food density would be represented in the distribution of the group, rather than the central nervous system of each individual? Animals may follow a rule as simple as "go to the closest morsel of food." Morsel magnitude might be reflected in the size of the groups formed simply because it takes longer to eat large morsels, resulting in a larger number of visible morsels near a source of larger food.

Indeed, the equations that describe a system are not always necessary to model it. For example, reaction-diffusion equations (see [9], especially chapters 14 and 15) predict patterns of diffusion in various systems (e.g., slime molds). But those systems can be simulated in cellular automata using simple, locally-defined rules.

In this paper, I demonstrate that it is not necessary to attribute complex representations of an environment at the level of the individual organism in order to explain complex group behavior. The approach of my simulation draws heavily on Simon's [8] notions of "satisficing" (rather than maximizing) algorithms, as expressed by Gigerenzer and his colleagues [2, 3], and Reynolds' simulations of flocking behavior [7] using simple rules at the individual level (e.g., try to stay within a certain distance of your neighbors without colliding with them).

In this simulation, I define a simple environment (a grid representing a pond), and various numbers of organisms (see Figure 1). For the sake of clarity, I will call the organisms "ducks" throughout this paper. In addition, food sources disperse food at given rates and of given magnitudes. In the simulation, individual ducks follow simple rules and principles of collision avoidance. Using only simple rules, it is possible to observe the same sort of behavior found in groups of ideal free ducks: when the simulated ducks interact, "probability matching" emerges.

2 Simulation 1: A nonrepresentational approach

Gallistel [1] presents a computational model that accurately predicts the behavior of foraging animals (actually, Myerson and Miezin's model [6]).[1] However, the model assumes that individual organisms are able to represent the food density at each food source. Thus, its accuracy is the result of its circularity: probability matching occurs because animals can represent and compare the food densities of multiple food sources. But what if we begin with a simpler behavioral model? Gallistel's model does not consider the possible contribution of the structure of external factors (other than food) on the behavior of animals (e.g., the distance between sources, the behavior of other animals).

---

[1]Their computational model consists of a set of equations which predict probability matching by individual organisms. To my knowledge, neither Myerson and Miezin nor Gallistel have conducted any simulations.

2.1 Method

2.1.1 Environment

In the first simulation, the environment was a 28 by 28 grid (the "pond") with two sources of food. The sources' locations were fixed. Source 1 was located at the center of the top edge of the pond. Source 2 was located at the center of the bottom edge. Three characteristics of the sources could be specified at the beginning of the simulation: the rate of dispersal from the source (actually the interval between dispersals, so that a rate of "2" is less than a rate of "1"), the size of the area into which food from a source could appear, and the magnitude of the "morsels" of food. For this simulation, when a duck made contact with a morsel of food, the duck would remain stationary until it was finished "eating." Eating time, in update cycles, was defined as the magnitude of a morsel of food; given a morsel of magnitude 5, a duck eating that morsel would remain stationary for 5 update cycles.

At the beginning of a simulation, a specified number of ducks was randomly distributed throughout the pond. At each time step, or cycle, food was distributed from a source if the cycle number was divisible by the its rate of dispersal. The constraints on dispersal were that the food could be randomly placed within a specified area around the source, and had to be placed on an empty point in that area. Subsequently, the locations of the ducks were updated in random order, in accordance with the rules described in Section 2.1.2

2.1.2 Individual rules and constraints

Duck behavior was determined by two rules:

1. If a duck contacts food, it remains stationary for a number of cycles equivalent to the magnitude of the morsel of food.
   Otherwise:

2. Approach the nearest morsel of food.

Initially, I defined five rules for individual ducks to follow that I thought would result in probability matching behavior. One rule involved seeking eating ducks when there was no available food. While such rules make the simulator more visually interesting, and possibly more realistic (since the

4

ducks do not stop moving when there is no food in the environment), they are redundant. Eliminating them yields the same result. Therefore, I used only these two rules.

In addition, I used two general principles of object avoidance:

1. If a duck is about to collide with another duck, the lesser of the vertical and horizontal components of its heading is modified (or one is chosen randomly if they are equal):

   (a) If the component is less than that of the duck's current position, it is decremented.

   (b) If the component is greater than that of the duck's current position, it is incremented.

   (c) If the component is equal to that of its current position, it is incremented or decremented (determined randomly).

2. If a collision is still imminent, the duck stops.

Without principles of object avoidance, a duck cannot avoid other, possibly stationary, ducks between it and a piece of food, and must "wait" for the others to move (although even with these principles, they must sometimes wait, if all points adjacent to them in the direction of the food are occupied by other ducks).

2.1.3 The simulator

The simulator was written in C on a Sun workstation, and uses the X Window libraries for graphics. The program is launched from a command line, where the number of ducks, the number of food sources (1 or 2), and the rates and magnitudes of each source can be specified. Figure 1 shows an example of the simulator screen. The squares at the top (labeled "S1:rate+", etc.) are buttons. The user can click on these to increase or decrease the rate and magnitude characteristics of each source interactively during a simulation. The effects can be observed visually in the "pond" area as well as quantitatively in the area below. The user can also add morsels of food directly into the pond by clicking on an empty location. The simulator also produces ASCII output recording the state of the simulator at each cycle.
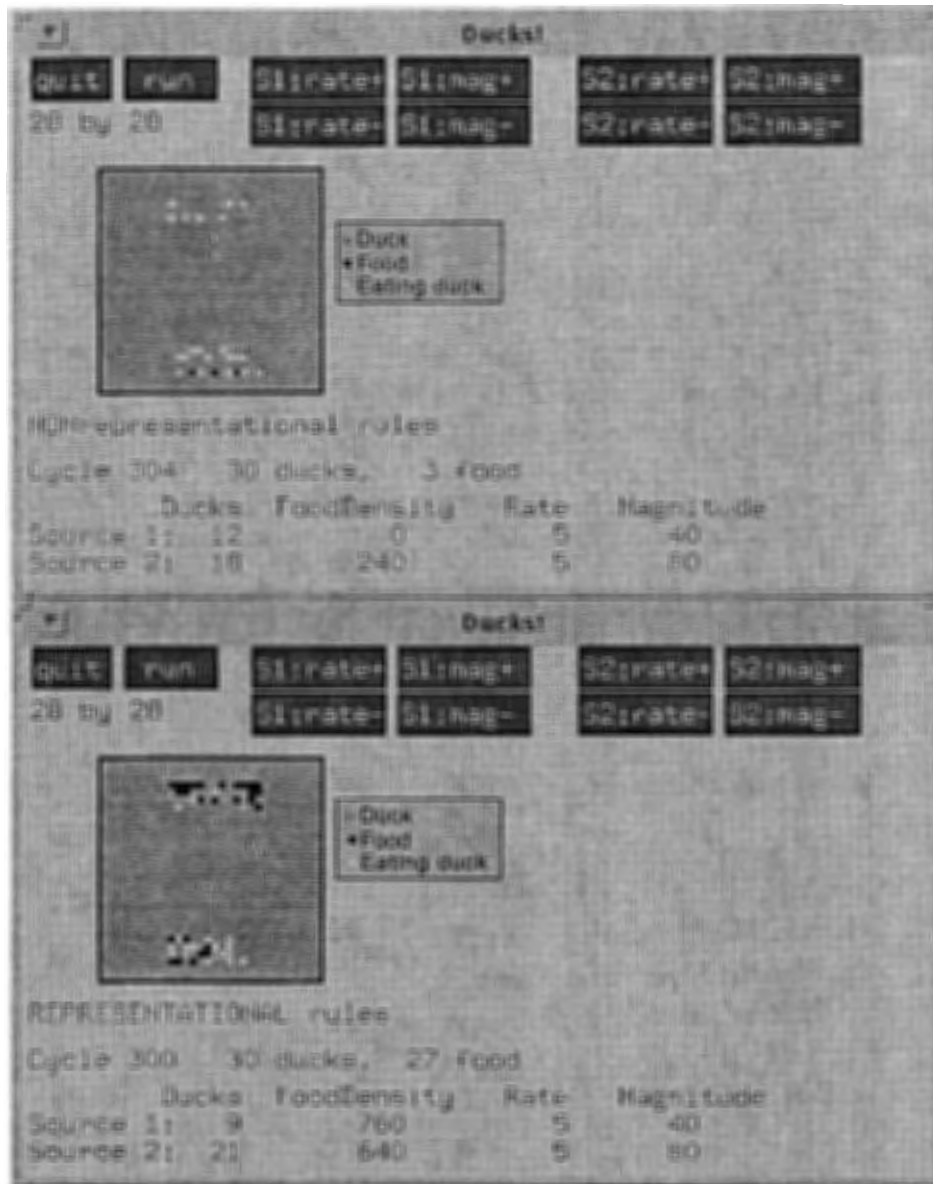
Figure 1: **The simulator window.** Parameters are set to those described in the second example for Simulation 1. The optimal numbers of ducks would be 10 at source 1 and 20 at source 2. The simulation in the top panel used only the nonrepresentational rules described in Section 2. In the representational simulation (lower panel), each duck acted on representations of food density at each source. Note that in the lower panel many ducks are crossing the pond, and that many more morsels of food are available. This is due to ducks switching sources when the density of the opposite source becomes greater than that of the current source. More rules and constraints would be required to prevent ducks from, e.g., ignoring food close to them in order to go to the denser source. Thus, the simpler rules yield better results.

2.2 Results

It is important to note that the results of the simulation are entirely determined by the rules I defined. However, computing the probability for each duck's behavior quickly becomes a very difficult problem. The size of the pond, the distance between the sources, the size of the area a source disperses food into, the rate and magnitude values for the sources, and the number of ducks interact in a complex fashion.

Note the relationship between magnitude and rate of dispersal. A change in magnitude will not have any effect unless the magnitude is approximately a multiple of the rate, since food dispersed at time t can be consumed by time $t + magnitude + 1$ (the minimum time for a duck to move to an adjacent morsel of food is one update cycle). For a duck to change sources, the only food available in the environment must be from a different source. This condition must remain true until the duck is closer to the new source's food than any new food from its original source, since the duck will seek the closest food. Therefore, for the system to converge on the distribution of ducks predicted by food density, food can be neither too plentiful (in which case ducks have no reason to change sources), nor too scarce (in which case food will be consumed by a duck close to a source before other ducks can change sources). However, by varying only rate or magnitude, it is possible to observe behavior which closely resembles probability matching.

2.2.1 Differences in rate

Once a proper balance between the number of ducks and the magnitude of morsels has been found,[2] one can observe probability matching after changing the rate of one source. Here is a representative example:

> Given two sources with magnitudes of 30, one source with a rate
> of 2, and another with a rate of 10 (5 times slower than the first),
> a group of 30 ducks forms two groups of approximately 25 (near

---

[2]By trial and error so far – which is quite easy, since one can interactively adjust parameters during a simulator run. Please note, though, that there are wide ranges and combinations of parameter settings that "work." Parameter adjustments are necessary only when the chosen combinations make food too scarce or too plentiful at one or both sources.
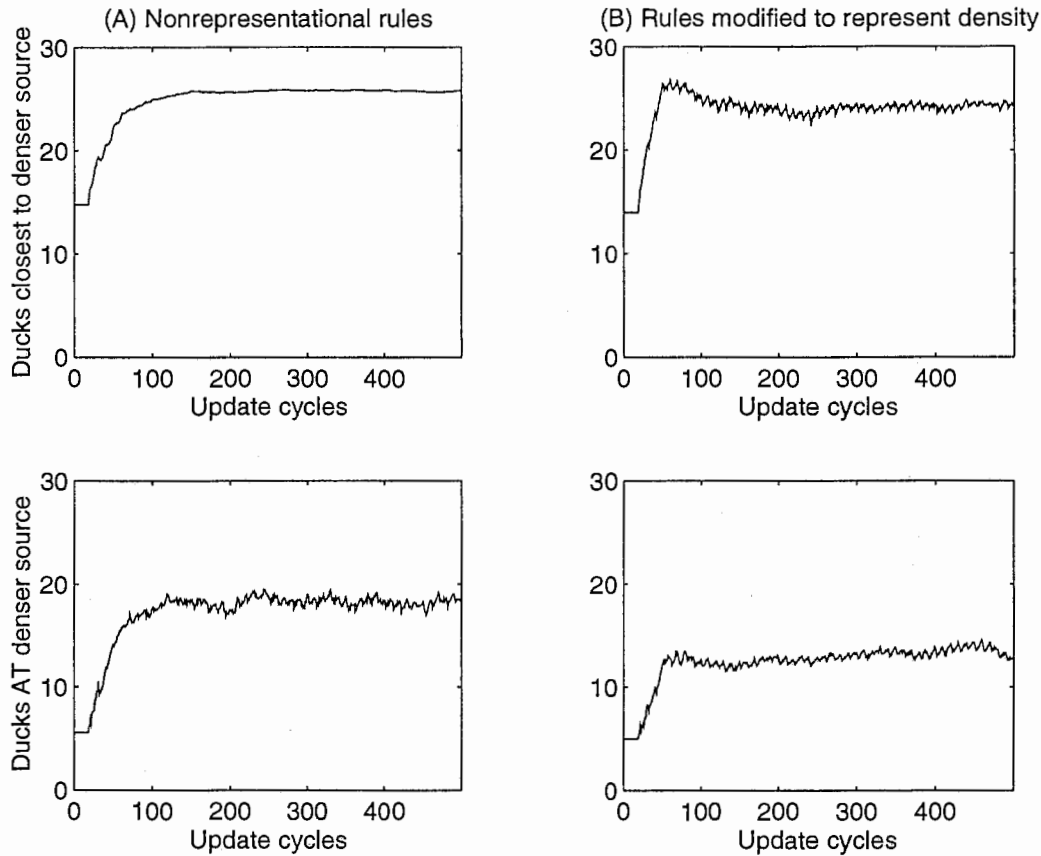
Figure 2: **Effects of differences in rate** (magnitude set to 10 for both sources; one source's rate set to 10, and the other's set 5 times faster to 2; 30 ducks) on the distribution of ducks (averages of 50 simulations by cycle). Results from Simulation 1, using only behavioral rules, are presented in the left column (A). Results from Simulation 2, where a representation of food density was added to the behavioral rules, are presented in the right column (B). The plots on the top row show the number of ducks closest to the denser (faster) source, i.e., the number of ducks in the half of the pond closest to that source. The plots on the bottom row show the number of ducks within the actual area the into which the denser source was distributing food. *In each case, the optimal number of ducks at the denser source is 25.* Note that the nonrepresentational simulation yields a result closer to the predicted result in both measures.
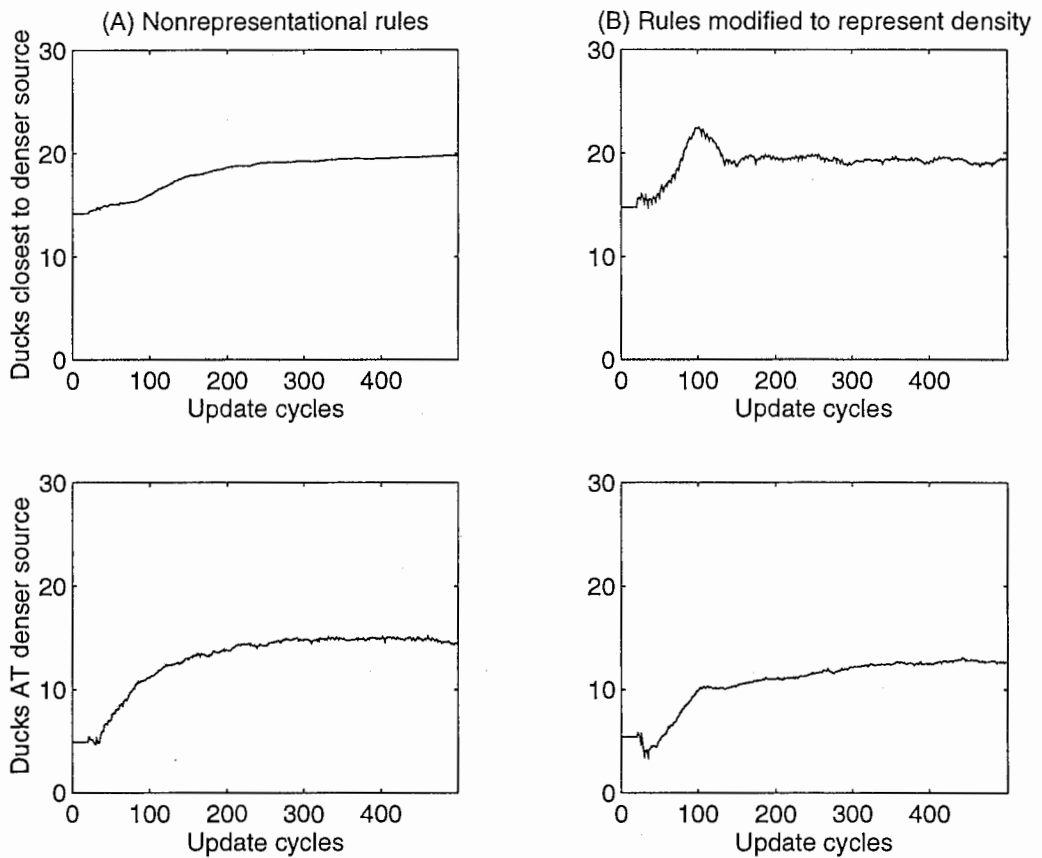
8

Figure 3: **Effects of differences in magnitude** (rate set to 5 for both sources; one source's magnitude set to 40, and the other's set to 80; 30 ducks) on the distribution of ducks (averages of 50 simulations by cycle). Results from Simulation 1, using only behavioral rules, are presented in the left column (A). Results from Simulation 2, where a representation of food density was added to the behavioral rules, are presented in the right column (B). The plots on the top row show the number of ducks closest to the denser source, i.e., the number of ducks in the half of the pond closest to that source. The plots on the bottom row show the number of ducks within the actual area the into which the denser source was distributing food. *In each case, the optimal number of ducks at the denser source is 20.* Note that the nonrepresentational simulation yields a result closer to the predicted result in both measures.

9

the first source) and 5 (near the slower source) within 100 update
cycles.

2.2.2 Differences in magnitude

The effects of magnitude are harder to model, as mentioned in section 2.2
For the difference between sources' magnitudes to affect the distribution of
ducks, it must be so large that food from the source with the larger mag-
nitude remains available long enough that ducks at the opposite source can
get closer to it before more food is distributed from the opposite source.
Thus, food density is difficult to calculate, and is a function of not just rate
and magnitude. The "swimming speed" of the ducks, and the distance be-
tween the sources also come into play. If magnitudes are set sufficiently high,
however, the relative contributions of those secondary factors decrease, and
probability matching emerges. For example:

> Given two sources with equal rates of 5, one source with a magni-
> tude of 80, and another with a magnitude of 40 (or, *16 x rate vs.*
> *8 x rate*), a group of 30 ducks forms two groups of approximately
> 20 (near the first source) and 10 after between (approximately)
> 100 and 300 update cycles.

2.2.3 Discussion

Although it is not clear how to equate update cycles with real time – with,
e.g., the real swimming and eating rates of ducks – the difference between
convergence times for rate and magnitude differences are similar, in general,
to those observed with real animals. Harper [4] found that distributions
of real ducks matched differences in rate within approximately 90 seconds.
The same group of ducks matched differences in morsel magnitude within
approximately 300 seconds. Compare these numbers with Figures 2 and 3:
differences in rate were matched after approximately 100 cycles, and differ-
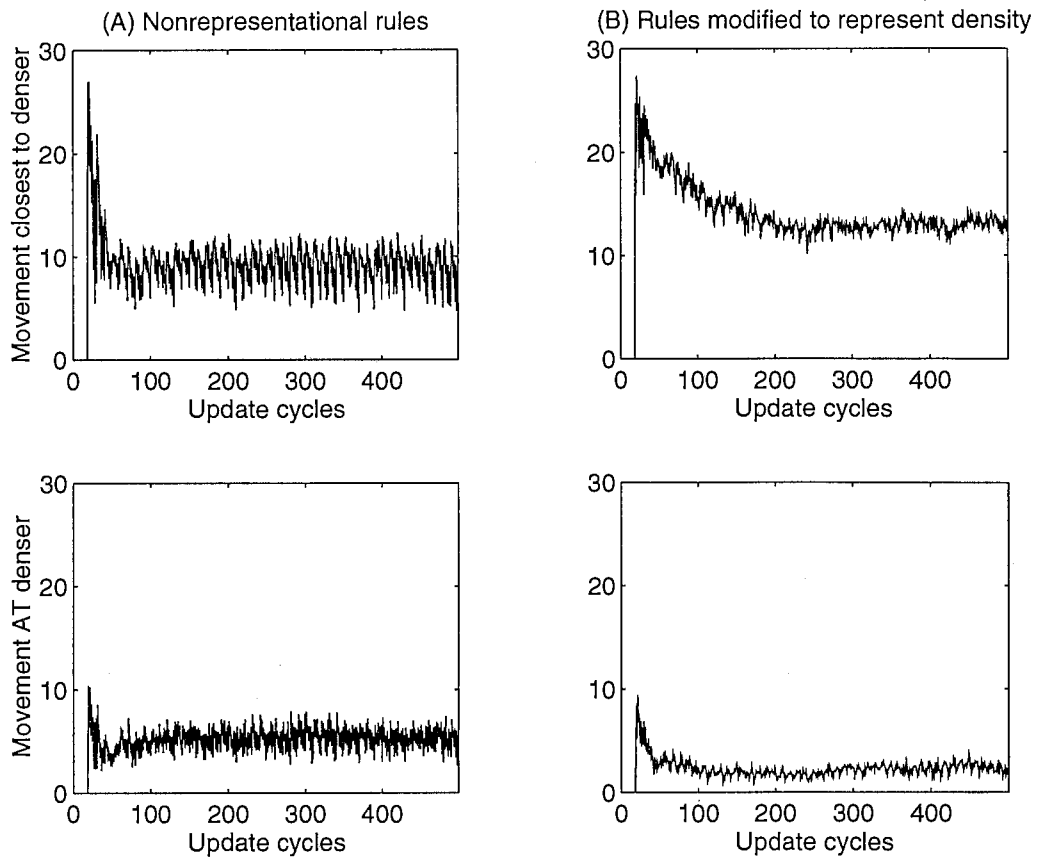ences in magitude were matched after approximately 300 cycles.

Figure 4: **Effects of differences in rate** (magnitude set to 10 for both sources; one source's rate set to 10, and the other's set 5 times faster to 2; 30 ducks) on the amount of movement in the system (i.e., the sum of squares based on change in position for each duck; averages of 50 simulations by cycle). Results from Simulation 1, using only behavioral rules, are presented in the left column (A). Results from Simulation 2, where a representation of food density was added to the behavioral rules, are presented in the right column (B). The plots on the top row show the amount of movement in the half of the pond near the denser (faster) source. The plots on the bottom row show the amount of movement within the actual area the into which the denser source was distributing food. Note that the total movement in the representational simulation is substantially greater than that in the non-represenational simulation. Note also that a much greater proportion of the movement in the representational simulation occurs distant from the food sources. As can be seen in Figure 1, unrealistic behavior emerges in the representational simulation – e.g., ducks pass up nearby food to move to the denser source.
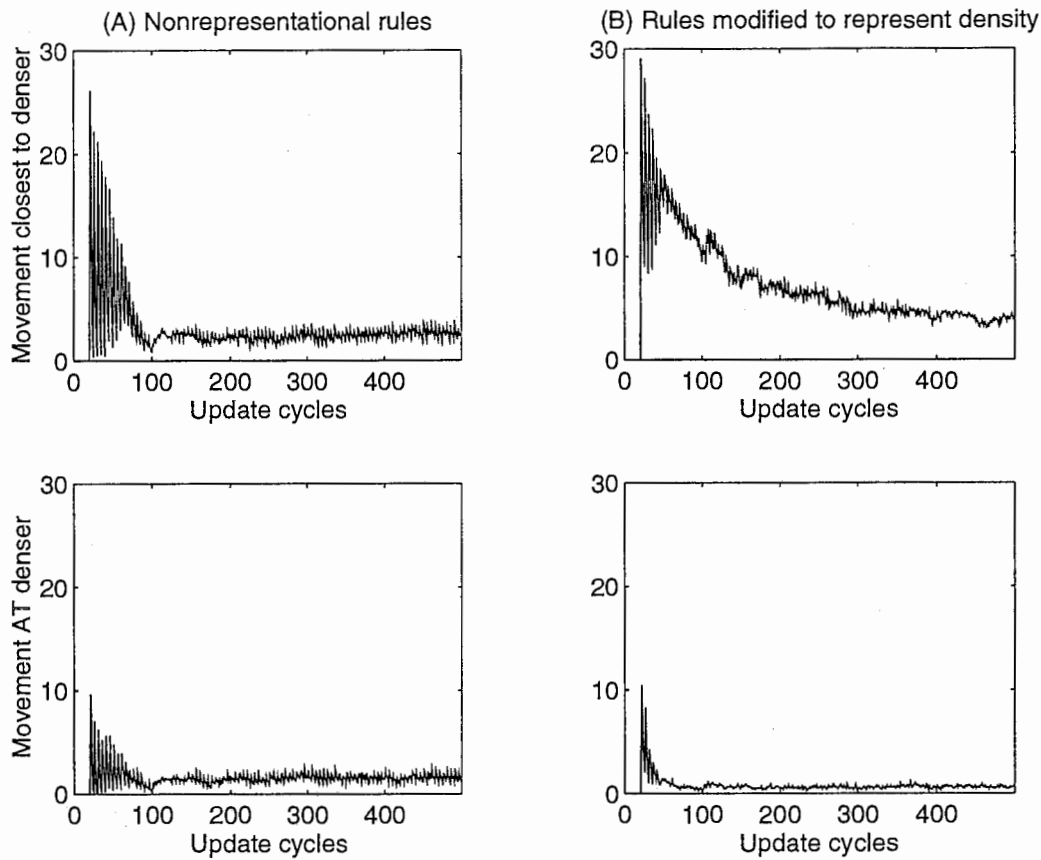
11

Figure 5: **Effects of differences in magnitude** (rate set to 5 for both sources; one source's magnitude set to 40, and the other's set to 80; 30 ducks) on the amount of movement in the system (i.e., the sum of squares based on change in position for each duck; averages of 50 simulations by cycle). Results from Simulation 1, using only behavioral rules, are presented in the left column (A). Results from Simulation 2, where a representation of food density was added to the behavioral rules, are presented in the right column (B). The plots on the top row show the amount of movement in the half of the pond near the denser source. The plots on the bottom row show the amount of movement within the actual area the into which the denser source was distributing food. As in the previous figure, there is more total movement in the representational simulation.

12

3 Simulation 2: A representational approach

In order to compare the results of Simulation 1 with the representational approach, I modified behavior rule 2. Instead of simply seeking food, ducks computed the current density of food at both sources, and then sought the closest morsel of food at the source with the highest density (density was simply the number of available morsels available at a source multiplied by the source's density). In every other respect, Simulation 2 was identical to Simulation 1.

3.1 Results and discussion

The results of Simulation 2 were usually similar to those of Simulation 1, except that it was even more susceptible to small changes in magnitude differences. This was clear from observing the simulator; there was much more movement in general, and at any given time, there were many more ducks in the area between sources. Also, the modified rule caused ducks to ignore the closest food – even immediately adjacent food – when the current density of the opposite source was greater than that of their location.

Simulations and 1 and 2 were conducted 50 times each on the two representative parameter settings described in Simulation 1. All simulations lasted 500 cycles. The average number of ducks at each source at each update cycle for the simulations with differences in rate are presented in Figure 2. The average number of ducks at each source at each update cycle for the simulations with differences in magnitude are presented in Figure 3.

The amount of movement in the Simulation 2 is compared with that of Simulation 1 in Figures 4 and 5, using the settings of the two representative examples reported in Simulation 1.

I cannot draw any strong conclusions from the relative instability and non-intuitive behaviors (e.g., bypassing food) introduced by attributing a representation of food density to the ducks. While it demonstrates that the rules used in Simulation 1 are made less effective by the addition, I have not yet completed an implementation of the complete model described by Myerson and Miezin [6] (for various reasons, but especially because it is not clear to me how to extend it to a group of animals rather than isolated individuals). Thus, the change to Rule 2 in Simulation 1 is perhaps not a valid implementation of the representational model.

I have conducted preliminary simulations with slightly modified versions of the rules, in an attempt to come closer to Gallistel's model. For example, instead of specifying that ducks change sources if the other source is denser, ducks calculated the density of each source, and then chose to switch sources probabilistically. This was accomplished by calculating the current density, d, of both sources and the proportion of food at source 1. Then a random number between 0 and 1, r, was generated, and the preferred source was determined by the rule:

> Source 1 is preferred if r is greater than the proportion of food at source 1;
> Otherwise 2 is preferred.

This change did not increase the stability of the system. When I changed the rules so that ducks did not compute the *current* densities but instead used the rates and magnitudes specified to calculate single densities for each source that did not attend to momentary changes, the system became less stable, in terms of the amount of movement and divergence from predicted distributions. The next step would be to weight the probabilities based on the distance of the sources from the duck (although this adds distance as a new factor – one that is not part of the representational model) or to give the ducks the ability to represent longer-term goals. With the current representational rules, ducks often change direction several times before reaching a source, since the density of each source changes almost every cycle. The crucial point is that it becomes more difficult to simulate probability matching when calculations and representations are incorporated into the behavior of the individual ducks (see Figure 1 for a comparison of behavior when representational and nonrepresentational rules are used): simulating a model like Gallistel's will require devising a set of behavioral rules in an ad hoc fashion to control behavior when, for example, the closest food is not at the denser source. That one can devise a set of rules that outperforms the mathematical model suggests that the model is unnecessarily complex.

4   Caveats and Conclusions

In these preliminary simulations, only two rules were used. Ducks were represented as single pixels, and I made no attempt to model any physical con-

14

straints on duck behavior (e.g., given a change in desired heading, how long does it take to turn, and what is the turning radius?). Nor have I considered pragmatic constraints that would exist in a real environment (e.g., line of sight; ducks were given the ability to determine which morsel of food in the environment was closest to them – even when there were other ducks directly between them and the food).

Gallistel's [1] explanation of probability matching in groups takes into account evidence about the behavior of individual animals in isolation. Individual animals such as rats appear to determine subjective reward magnitudes when faced with multiple sources of food. The probability of food dispersal from a source predicts how long they will wait at that source before checking another. Another possible aspect of duck behavior I have not considered is how long ducks will stay at a source without eating, even if there is more food available from it than another.

It is possible that the resemblance of the simulations to the behavior of real animals is simply an artifact of an extremely simplified environment and overly-simple definitions of individual behavior. Given the similarities of the current simulation to real behavior, this seems unlikely. However, simulations with more elaborately defined environments and simulations of the behavior of individual organisms in isolation are needed to test these possibilities.

In the meantime, the current results support the notion that optimal individual representations are not necessary to explain complex group behavior. Quantitatively-equivalent, "satisficing" algorithms, based on interactions between individuals, require us to attribute less complexity at the individual level. While explanations based on such algorithms may not turn out to be accurate, they should be considered along with more complex explanations. Finally, the simulator itself is a useful tool for preliminary tests of predictions about the behavior of real organisms.

Acknowledgments

References

[1] Gallistel, C. R. (1990). The Organization of Learning. Boston: MIT.

[2] Gigerenzer, G., Hoffrage, U., and Kleinbolting, H. (1991). Probabilistic mental models: A Brunswikian theory of confidence. Psychological Review, 98, 506-528.

[3] Goldstein, D. G. (1994). The Less-is-More Effect in Inference. Unpublished Master's thesis, University of Chicago Department of Psychology.

[4] Harper, D. G. C. (1982). Competitive foraging in mallards: Ideal free ducks. Animal Behaviour, 30, 575-584. (Cited by Gallistel.)

[5] Lea, S. E. G., and Dow, S. M. (1984). The integration of reinforcements over time. In J. Gibbon and L. Allan (Eds.), Timing and Time Perception (pp. 269-277). New York: Annals of the New York Academy of Sciences [Vol. 423]. (Cited by Gallistel.)

[6] Myerson, J. and Miezin, F. M. (1980). The kinetics of choice: An operant systems analysis. Psychological Review, 87, 160-174. (Cited by Gallistel.)

[7] Reynolds, C. W. (1987). Flocks, herds, and schools. A distributed behavioral model. Computer Graphics 21(4) (SIGGRAPH '87 Conference Proceedings), ACM, New York, 25-34.

[8] Simon, H. A. (1957). Models of Man. New York: Wiley.

[9] Winfree, A. T. (1980). The Geometry of Biological Time. New York: Springer-Verlag.