Honey Bee Swarm Cognition: Decision-Making Performance and Adaptation

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ABSTRACT

A synthesis of findings from neuroscience, psychology, and behavioral biology has been recently used to show that several key features of cognition in neuron-based brains of vertebrates are also present in bee-based swarms of honey bees. Here, simulation tests are administered to the honey bee swarm cognition system to study its decision-making performance. First, tests are used to evaluate the ability of the swarm to discriminate between choice options and avoid picking inferior "distractor" options. Second, a "Treisman feature search test" from psychology, and tests of irrationality developed for humans, are administered to show that the swarm possesses some features of human decision-making performance. Evolutionary adaptation of swarm decision making is studied by administering swarm choice tests when there are variations on the parameters of the swarm's decision-making mechanisms. The key result is that in addition to trading off decision-making speed and accuracy, natural selection seems to have settled on parameters that result in individual bee-level assessment noise being effectively filtered out to not adversely affect swarm-level decision-making performance.

Keywords: *Apis Mellifera, Honey Bees, Nest-Site Selection, Swarm, Swarm Cognition*

1. INTRODUCTION

The "collective intelligence" or "super-organism" perspectives have been used for both animals and humans to discuss fully integrated group functioning, especially group decision-making (Hölldobler & Wilson, 2008, 1990; Levine et al., 1993; Franks, 1989; Seeley, 1989, 1995; Hinsz et al., 1997; Wilson, 2000; Camazine et al., 2001; Surowiecki, 2004). But, how does a group of organisms implement a "mind" that supports group decision-making? Recently, this question has been partially answered. Viewing the honey bee super-organism as a single decision-maker, a detailed explanation of the honey bee nest-site selection process has been used to identify the key elements and functional organization of swarm cognition (Passino et al., 2008). It was shown that the swarm has identifiable elements that correspond to neurons, action potentials, inter-neuron communications, lateral inhibition, short-term memory, neural images, and layers of processing (Kandel et al., 2000). Functional similarities to the networks of neurons that perform certain attention, perception, and choice functions (Gazzaniga et al., 1998; Kandel et al., 2000) in solitary animals were identified. It was shown that the swarm's short-term memory ("group memory") is on average a representation of the relative quality of the

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discovered nest sites that leads to good choice performance. Then, two basic properties of the swarm's choice process were tested: discrimination (the ability to distinguish between nest sites of different quality) and distraction (the ability to ignore nest sites of inferior quality). The focus of this paper is to analyze swarm decision-making performance and adaptation to provide additional evidence that bee-based swarms have a cognition process that shares key features with neuron-based brains.

The key experimental work in the area of honey bee nest-site selection is in (Seeley & Buhrman, 1999; Camazine et al., 1999; Seeley & Buhrman, 2001; Seeley, 2003; Seeley & Visscher, 2003, 2004a). A number of models of the nest-site selection process have been published. First, there are the ODE models introduced in (Britton et al., 2002) to study the issue of whether bees make direct comparisons between the qualities of more than one nest in order to make a decision (which they do not). There is a discrete-time population matrix model introduced in (Myerscough, 2003). A simulation model that was validated for a range of experiments (those in (Seeley & Buhrman, 1999; Camazine et al., 1999; Seeley & Buhrman, 2001; Seeley, 2003; Seeley & Visscher, 2003, 2004a)) is introduced in (Passino and Seeley, 2006) and used to study the speed-accuracy trade-off in the choice process. In Perdriau and Myerscough (2007) the authors introduce a density-dependent Markov process model of honey bee nest-site selection and study the effects of site quality, competition between sites, and delays in site discovery. Next, the work in (Janson et al., 2007) introduces an individual-based model and studies the swarm's scouting behavior and the impact of distance on choice. Ant colonies performing nest-site selection have some broad similarities to the bees' nest-site selection process (e.g., a speed-accuracy trade-off), and corresponding models and simulations have been developed (Mallon et al., 2001; Pratt et al., 2002; Franks et al., 2003; Pratt, 2005; Pratt et al., 2005). Finally, note that recently a common framework was introduced to study the optimality of decision-making in the brain along with nest-site selection in both ants and bees (Marshall et al., 2009).

In this paper, the simulator from (Passino & Seeley, 2006) is used to administer tests to the swarm to evaluate its decision-making performance and adaptation. First, basic properties of discrimination and distraction and their interaction are studied by administering swarm choice tests. Then, it is shown that choice performance analogous to what humans possess is found if the Treisman feature search test for humans (Treisman & Gelade, 1980) is given to the swarm. In particular, the Treisman test illustrates how swarm cognition dynamics operate in parallel in early processing and how cognition delays can occur in the presence of many inferior choices. Next, it is determined whether swarms exhibit "irrational" choice behavior commonly found in (individual) human decision making (Luce & Suppes, 1965; Huber et al., 1982; Tversky, 1972; Simonson, 1989; Simonson & Tversky, 1992) in the presence of context-dependent effects (i.e., certain patterns of choice alternatives that can conspire to mislead the decision-maker). Irrationality has already been studied in the field of behavioral ecology. In hoarding gray jays, simultaneous choice errors decrease as the rate of availability of choices decreases, since then choice errors are costly (Waite, 2001; Waite & Field, 2000; Waite, 2002). Honey bees and gray jays have been shown to exhibit context-dependent decision making (Shafir et al., 2002). In these studies errors ("irrationality") seem to arise due to sensory noise, cognitive processing limitations, and physical constraints (which all cause choice errors in nest-site selection also). Context-dependence has also been studied for human group decision making (Steiner, 1966; Laughlin & Ellis, 1986; Kerr & Tindale, 2004; Hastie & Kameda, 2005) as summarized in (Hinsz et al., 1997). Here, analogous to the studies in (Ratcliff et al., 1999; Ratcliff & Smith, 2004; Roe et al., 2001; Busemeyer & Townsend, 1993) for humans, context-dependent decision making is studied for a reaction-time test (quick choice of the best-of-N nest sites). For a very wide variety of nest-site quality patterns,

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simulations here show that the swarm cannot be tricked into misordering its choice percentages in relation to the nest-site quality pattern. This implies that violations of strong stochastic transitivity (Luce & Suppes, 1965) will not occur. Next, it is shown that for a special nest-site quality pattern (where a discrimination-distraction interaction is induced) the attraction effect (Huber et al., 1982) can occur. However, this leads to *improved* choice performance.

Finally, using a cognitive ecological perspective (Dukas, 1998) swarm-level choice performance is studied when individual-level bee behavioral parameters are perturbed (a "pseudo-mutated" swarm (Passino & Seeley, 2006)). Simulations show how natural selection seems to have settled on cognition mechanisms that balance the speed and accuracy of nest-site choice and filter error-prone individual bee decisions. From a broad perspective, this last part of the paper provides an initial synthesis of ideas from group decision making and cognitive ecology (Dukas, 1998), which has been previously thought to only apply to neuron-based brains.

2. NEST-SITE SELECTION BY HONEY BEES

The simulation model from (Passino & Seeley, 2006) is used here to administer all choice tests and to study adaptation. This model was validated using the experiments in (Seeley & Buhrman, 1999; Camazine et al., 1999; Seeley & Buhrman, 2001; Seeley, 2003; Seeley & Visscher, 2003, 2004a) and is summarized here to explain the nest-site selection process and set the notation for our analysis.

In nest-site selection (reviewed in (Seeley & Visscher, 2004b; Seeley et al., 2006; Passino et al., 2008)), the colony splits itself when the queen and about half the old colony depart and assemble as a cluster nearby, typically on a tree branch. Assume $B = 100$ "scout" bees take on different roles (explorer, observer, committed, rester, and dead) in the nest-site selection process that occurs on the surface of the cluster of bees. Let k be the time step index. A scout bee can conduct one expedition from the swarm cluster per time step. When a scout, functioning as an "explorer," successfully finds a candidate nest site (e.g., a hollow of a tree) it evaluates its attributes to form a quality assessment based on cavity volume, entrance height, entrance area, and other attributes that are correlated with colony success. Denote the quality of site j as $N^j \in [0,1]$ with "1" representing a perfect site. Let the position of scout bee i be θ^i, and let $J(\theta)$ denote the "landscape" of site quality, with $\theta = [0,0]^T$ the position of the cluster. Then $J(\theta^i) = N^j$ if scout i is at site j. Scout i has assessment noise $w^i(k)$, and a quality threshold $\epsilon_t = 0.2$ below which it will ignore a site. Hence, scout i's assessment of a site at time step k is $S^i(k) = J(\theta^i(k)) + w^i(k)$, if $J(\theta^i(k)) + w^i(k) > \epsilon_t$, and zero otherwise. Here, $w^i(k)$ is uniformly distributed on $(-01, 01)$ to represent errors up to $\pm 10\%$ in the scout's assessment of nest-site quality (a normal distribution is inappropriate because large but unlikely deviations from the mean do not seem to exist in nature). Any scout bee that finds an above-threshold nest site dances for it (recruits other bees to it) and hence becomes "committed" to that site. Bees die with a small probability $p_d = 0.0016$ on each expedition so that less than 10% die over the whole nest-site selection process.

An unsuccessful explorer returns to the cluster and seeks to observe a dance. The time step that scout bee i first discovers site j is k_j^i and if the assessed quality of the site is above the quality threshold, this bee returns to the cluster and dances with a "strength" (number of waggle runs, with each run communicating the angle and radial distance to the nest site via the angle the run makes relative to the sun and the duration of the run) of $L^y(k_j^i) = \gamma S^i(k_j^i)$

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waggle runs where $\gamma = 150$; hence dance strength is correlated with nest quality. The dances recruit other bees to visit the site. After dancing, this committed bee returns to the site, and then back to the cluster, possibly making several such round trips between the swarm cluster and nest site; however, each time it returns to the cluster it dances on average $\epsilon_s = 15$ fewer waggle runs than the previous time. The sequence of waggle runs produced by scout bee i over the whole process is L^i and the total number of waggle runs produced on the cluster for all sites at time step k is $L_t(k)$. Let $\sum L_t$ denote the total number of waggle runs over the entire process. A sequence of dances by one scout bee for one site, from the time of the initial dance to when the dance strength decays to zero, is called a "dance decay series." After a committed scout's dance strength has decayed to zero it rests and rejoins the process (by seeking to observe a dance) at each expedition with a probability $p_m = 0.25$. Scout bees that seek to observe a dance will end up exploring instead with probability $p_e(k) = \exp\left(-\frac{1}{2}\frac{L_t^2(k)}{\sigma^2}\right)$ where $\sigma = 4000$, representing that when there is not much dancing on the cluster (small $L_t(k)$, meaning few good sites have been found), then there will be more exploring, and vice versa. There are $B_r(k)$ resters, $B_e(k)$ explorers, $B_o(k)$ bees that seek to observe, $B_u(k) = B_o(k) + B_e(k)$ uncommitted bees, and $B_c(k)$ committed bees. With probability $1 - p_e(k)$ observer bees will observe dances, and with probability $p_r(k) = \frac{L^i(k)}{\sum_{i=1}^{B_c(k)} L^i(k)}$ they will be recruited by the i^{th} dancing bee; this means that recruits will be proportioned across candidate sites based on the site's relative proportion of recruiters, with better sites thereby getting more recruits. Bees recruited to site j will visit and dance for it back at the cluster according to their own assessment, as described above.

Key parts of the whole process are occurring simultaneously with the scouts performing and observing dances on the cluster and sensing at each candidate nest site the number of other bees at the site. When the quorum threshold $\epsilon_q = 20$ is reached at one of the sites (the time at which quorum achieved is called the "agreement time" and it is denoted with T_a), the bees there return to the cluster and produce piping signals that elicit heating by the quiescent (non-scout) bees in preparation for flight. Eventually, the entire swarm lifts off and flies to the chosen site, guided by the scout bees. There is significant time-pressure to complete the nest-site selection process as fast as possible since weather and energy losses pose significant threats to an exposed colony. However, enough time must be dedicated to ensure that many bees can conduct independent evaluations of the site and enough must agree that it is the best site found. Hence, during nest-site selection the swarm optimizes a balance between time minimization and site quality choice maximization (Passino & Seeley, 2006).

Each expedition by a scout bee is assumed to take 30 min, and the maximum amount of time for the swarm to make its choice is set at 32 hrs, so there are up to 64 time steps. Due to the possibility of simultaneous quorum achievement at two or more sites there can be "split decisions." In this case, the process is restarted by having the swarm lift off, fail to fly away, and then reform the cluster. Also, the process can fail to come to agreement before 64 time steps are completed, which is called a "no-decision failure." These failures can arise if a site of sufficient quality, one that will generate a recruitment rate that will assemble the required

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ϵ_q bees at a nest site, is not discovered early enough.

3. DISCRIMINATION AND DISTRACTION PROPERTIES

Viewing the swarm as a cognitive unit, its choice performance is evaluated in this and the two following sections. Choice performance of swarms is considered for several landscapes of nest-site quality. For each landscape and each choice test, 100 nest-site selection processes that terminate with a single site chosen are used. Then statistics are computed from the resulting data.

3.1 Discrimination Amplification

Let all sites have zero quality, except sites 5 and 6, which both start out at a quality of $N^6 = N^5 = 0.65$ and differentially move to 0.4 and 0.9. When both sites are at a quality of 0.65, the top-right plot of Figure 1 shows that it is equally likely that each site is chosen. As the two sites have increasingly different quality values, the swarm is increasingly better at discriminating between them. When the site quality difference is above 0.3 the swarm is always correct in its choice of the best site. Next, see the top- and bottom-left plots of Figure 1. There is a slight decrease in the median value of T_a and mean value of $\sum L_t$ since in this case the quality of site 5 is much lower so that it is not nearly as viable of a candidate; hence, it is easier to choose the best site (i.e., without as much deliberation that takes time). The bottom-right plot of Figure 1 shows that the number of bees not visiting sites goes up slightly as differential quality increases. This demonstrates that fewer bees are needed to join the process of selection when there are clear quality differences in the field of possible nest site qualities.

The results in Figure 1 also show that discrimination ability goes up relative to Figure 3 in Passino et al. (2008), indicated by increased slope on the percentage of times the correct site (site 6) is chosen as they move away from each other (in the initial part of the top-right plot, the slope is approximately (1-0.5)/0.3=5/3, compared to 5/4 when the sites start at 0.75). Hence, discrimination is better when site qualities are lower since mistakes are more costly. Notice that compared to Figure 3 in Passino et al. (2008) there is more coupling in the process here due to more bees abandoning the low quality site and switching to the high quality site (here, for some values of differential quality about 11/40=27.5% dance for two sites).

3.2 Effect of Number of Distractors: Treisman Feature Search Test

Let $N^6 = 1$ and $N^5 = 0.55$, then successively add sites 1, 2, 3, and 4 as additional distractors of quality 0.55. So, there are a total of 2, 3, 4, and 5 distractors. This is a Treisman feature search test (Treisman and Gelade, 1980) with one "target" (the best site) that should be chosen, and a variable number of distractors. The results in Figure 2 show that as more distractors of such a low quality are added there is little effect on the percent of correct choices (see top-right plot) relative to when there are only two distractors; however, this comes at the cost of an increased mean $\sum L_t$ for the swarm to try to resolve the differences (see bottom-left plot). Treisman and others took this as evidence of early *parallel* neural processing of alternatives, early enough that it was not at the level of consciousness. Clearly, the swarm is processing the distractors in parallel also and this test shows that this has a positive effect on swarm choice performance.

The main result, however, comes from comparing with the case where everything is the same as in the previous test, but $N^6 = 0$, that is, when the target is removed. In standard feature search tests human subjects are asked to decide if the target is there or not, something that cannot be requested from the swarm. In-

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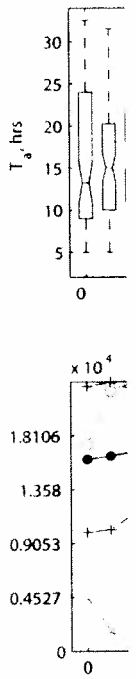

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Figure 1. Amplified discrimination effect: Top-left: middle line in each box is the median value of T_a, boxes with notches that do not overlap represent that the medians of the two groups differ at the 5% significance level (i.e., a pairwise statistical hypothesis test), whiskers (dashed lines) represent 1.5 times the interquartile range, and outliers are designated with a "+". Top-right: percentage of times each nest site is chosen (black lines), with site 1 designated by ▷ ("tR" represents "triangle right", a right-pointing triangle), site 2 by △ ("tU" represents "triangle up"), site 3 by ◇ ("dia"), site 4 by □ ("sq"), site 5 by ○, and site 6 by ∗. The gray lines with markers show the relative site qualities, $N^i / \sum_i N^i$. Bottom-left: left-vertical axis and the black lines show the mean $\sum L_i$ (solid line, dots), and its standard deviation (dash-dot line, + marker), while gray lines and right-vertical axis show the number of split decision (×) and no-decision (○) cases that occur for the 100 nest site selection processes that terminate with a single choice. Bottom-right: left-vertical axis and the black lines show the mean number of bees out of the 100 total that visit 0 sites (designated with ▷), 1 site (△), 2 sites (◇), 3 sites (□), 4 sites (○), 5 sites (∗), and 6 sites (×), and right-vertical axis shows via the gray lines the mean number B_c of committed scouts (×) and mean number of explorers B_e (+) at the agreement time T_a.

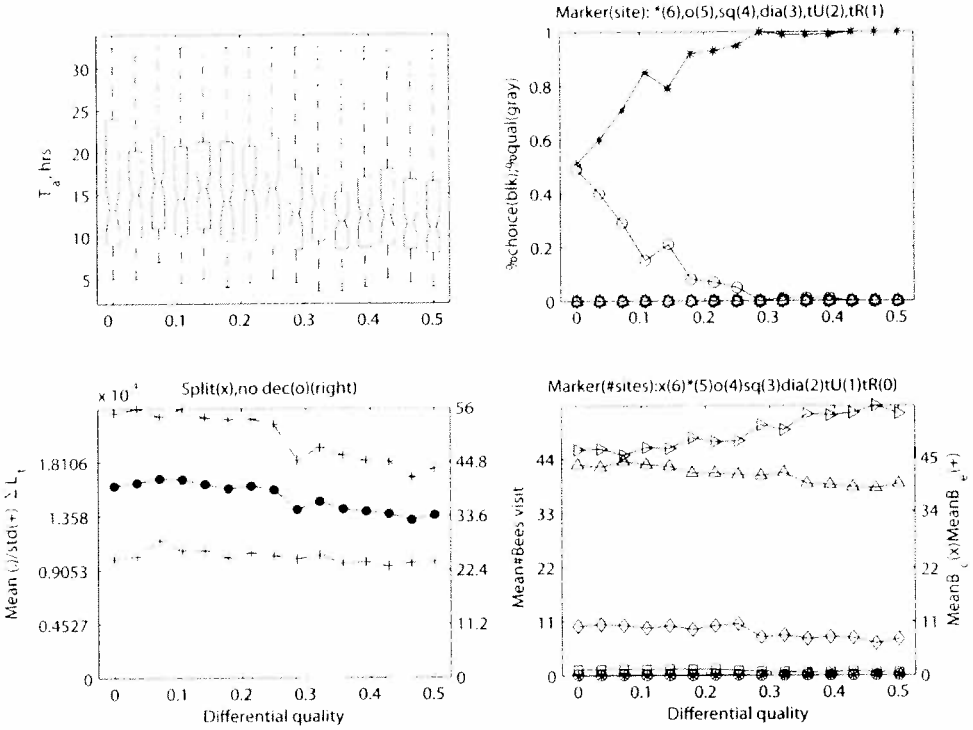

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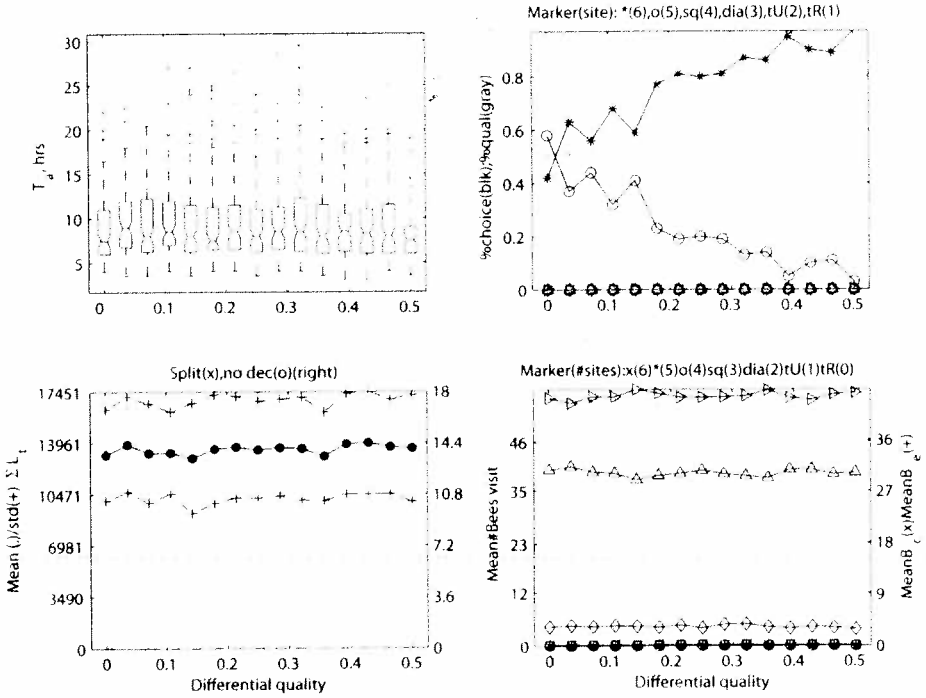
Figure 2. Effect of number of distractors, with perfect site present (see Figure 1 caption for axes explanation)



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stead, the swarm comes to a decision for this case and the results are compared to the last case. The results in the top-right plot of Figure 3 show that as expected, with two distractors each is chosen 50% of the time, 3 are each chosen about 33% of the time, 4 are chosen around 25% of the time, and 5 about 20% of the time. The mean $\sum L_t$ increases with more distractors but the median T_a goes up, then comes down since it becomes easier to make the errors that occur with 5 distractors. Also, comparing Figures 2 and 3, the median T_a values are *higher* for the case when there is no target compared to when the target is present. An analogous result is obtained in tests for humans, and Treisman hypothesized that humans switched to a "sequential search mode" where by a process of elimination they decided that the target was not present (Treisman & Gelade, 1980; Gazzaniga et al., 1998). For the swarm such a mode switch is not possible. The swarm simply takes longer to decide due to the internal dynamics of the decision-making process being slowed by a more lengthy evaluation of the evidence gathered.

4. DISCRIMINATION-DISTRACTION INTERACTIONS

The tests in the last section were designed to illustrate *isolated* swarm discrimination abilities and distractor effects. In other nest-site quality landscapes, however, both effects are present and interact with each other as shown next.

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First, it is sho discriminatio except let site sites 5 and 6 b and differenti considered to be chosen. N Figure 4 the quality range as similar) (relative to Fig al., 2008) and correct choice 1 and Figure discriminatio low quality di

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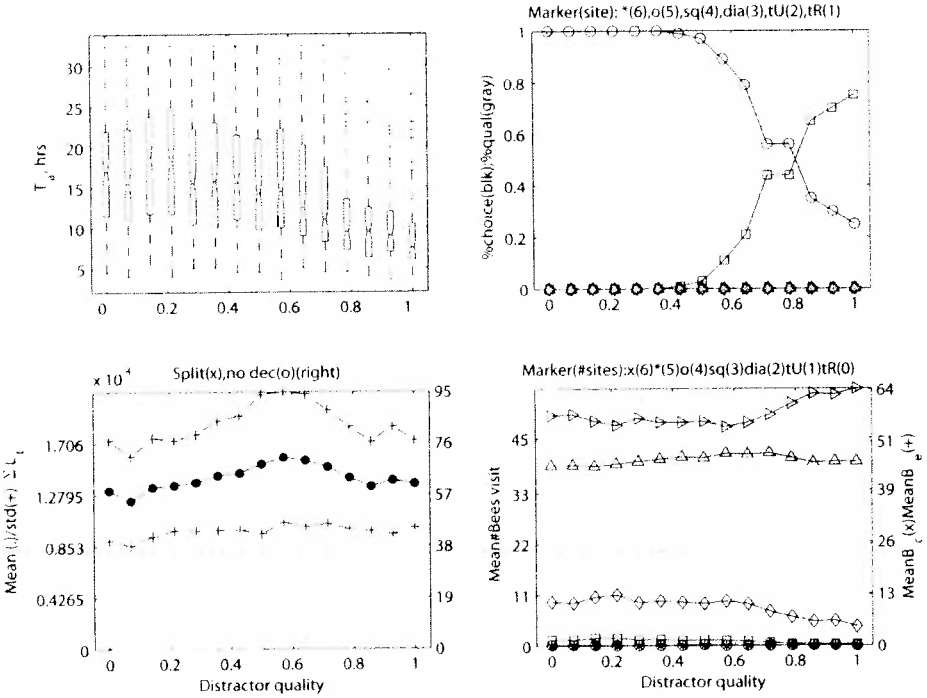
Figure 3. Effect of number of distractors, without perfect site present (see Figure 1 caption for axes explanation)



4.1 A Distractor Can Attenuate Discrimination

First, it is shown that distraction can attenuate discrimination. Let all sites have zero quality, except let site 4 have a quality of 0.5 and let sites 5 and 6 both start out at a quality of 0.75 and differentially move to 0.5 and 1. Site 4 is considered to be a distractor since it should not be chosen. Notice that in the top-right plot of Figure 4 the region of "generalization" (i.e., quality range where the swarm treats qualities as similar) (Gazzaniga et al., 1998) grows relative to Figure 1 and Figure 3 in (Passino et al., 2008) and the slope of the line representing correct choices is about 1 (lower than in Figure 1 and Figure 3 in (Passino et al., 2008)) so that discrimination is attenuated by the relatively low quality distractor. This attenuation occurs while all other key variables (e.g., median T_a and mean $\sum L_i$) stay relatively constant. This illustrates that the generalization effect is solely coming from the effect of site 4 as a distractor.

4.2 Discrimination Tries to Overcome Distraction

Let the quality of site 5 be 0.75, let the quality of site 4 vary as $N^1 = D \in [0,1]$ and consider site 4 to be a distractor for the range $D \in [0,0.75]$ since it should not be chosen for that range of values, but it is the best site for $D \in (075,1]$ when you can view site 5 as the distractor (this is a case of nonlinearly decreasing differential quality). Of course, you could view the basic

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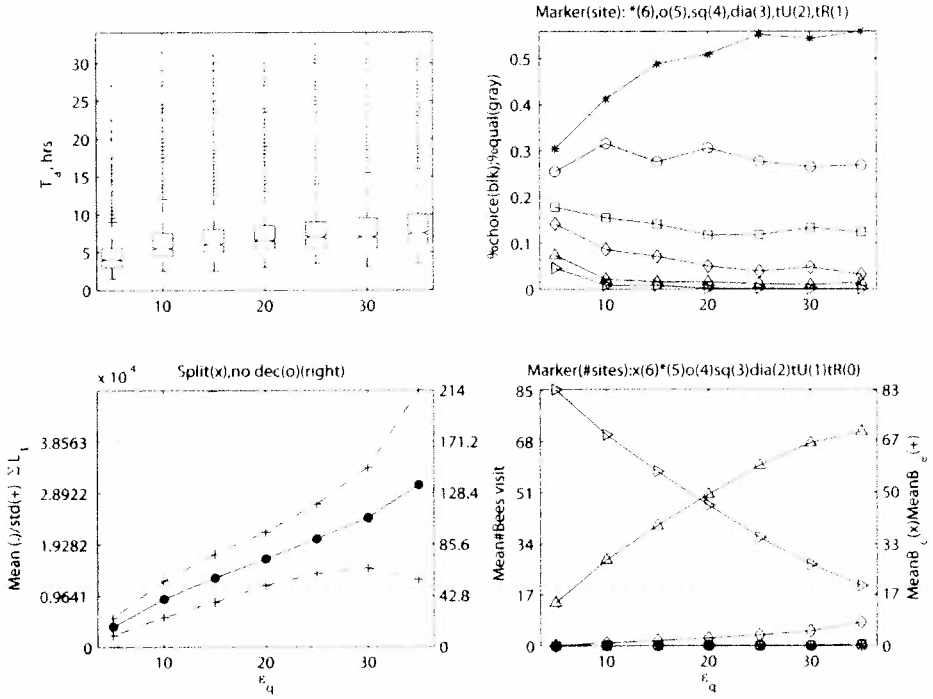
Figure 4. Distraction can attenuate discrimination (see Figure 1 caption for axes explanation)



task as one of discriminating between the two sites. The results are in Figure 5. First, note that discrimination level is asymmetric in the sense that the swarm is better at discriminating when $D \in [0, 0.75]$, but discrimination is not as good for $D \in (075, 1]$ (mistakes are not as costly in that region). There is a small region of generalization around 0.75. It is interesting that the median T_d values are relatively high until the quality of the sites approach each other, and then the amount of dancing $\sum L_t$ increases in order to discriminate between the sites, but then decreases as the sites move apart again. Also, the median T_d value decreases in the range $D \in [0.8, 1]$ (since it is easier to make a quick but incorrect decision) and note that there are fewer outliers. There are many no-decision cases when site 4 has a low quality; this is due to the difficulties of finding the *single* relatively good site 5. Overall, this shows that distraction tends to have an effect on choice performance degradation that discrimination tries to overcome (i.e., the "tension" between choice performance enhancement via good discrimination and choice performance degradation via distraction is balanced).

4.3 Context Dependence: Transitivity

A broad range of nest-site quality landscapes were tested to see if the swarm would ever misorder the percentages of choices for sites in comparison to the order of relative nest-site qualities. These tests included all the simulation results shown in the discrimination and distraction tests above, the general class of landscapes described at the beginning of the

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5. ADAPT OF SWAF PROCES

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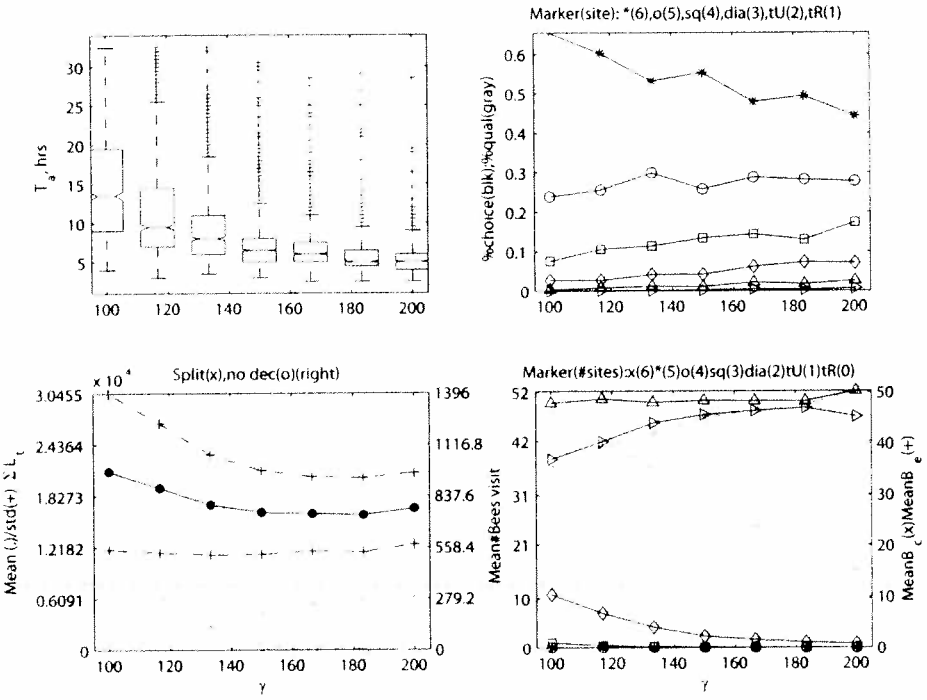
Figure 5. Nonlinear differential quality (see Figure 1 caption for axes explanation)



next section, the cases considered in (Passino & Seeley, 2006), and many landscapes not reported here. The tests were never able to "trick" the swarm: the percentage choice order is always given by the ordering of the relative qualities of the nest sites (to see this, review all plots of choice performance in this paper). Hence, the swarm never violates "strong stochastic transitivity" (Luce & Suppes, 1965) which can lead to choice errors.

5. ADAPTIVE TUNING OF SWARM COGNITION PROCESSES

To gain more insights into the mechanisms of swarm decision making, their evolutionary adaptation is studied. First, the adaptive tuning of the parameters of the individual bees' decision-making is studied. This helps to further validate the model and serves to show how speed accuracy trade-offs emerge from the adaptive tuning of the swarm's cognition process. Second, the effect of the amount of individual bee nest-site assessment noise on the swarm's choice performance and speed-accuracy trade-off is studied.

To study the adaptive tuning of individual bee-level behavioral parameters, their values are changed ("pseudo-mutated") from experimentally-determined ones, and the average time/energy costs and choice performance are evaluated. Six sites with qualities uniformly distributed on $[\epsilon_t, 1]$, where $\epsilon_t = 0.2$ is the threshold quality, are used. The randomly generated qualities are ordered so that site 1 is the lowest quality, site 2 is the second worst one, and so on, and this makes site 6 the best site. Each nest-site quality landscape generated this way is highly likely to produce interacting

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distraction and discrimination effects and hence generally more challenging choice tests than in (Passino & Seeley, 2006). Seven values of each behavioral parameter are considered, and for each of these, 1000 nest-site selection processes are run (each for a randomly generated landscape). Performance is characterized using statistics of the 1000 runs for each parameter.

5.1 Effect of Quorum Threshold Size

Figure 6 shows that small ϵ_q values result in fast decisions (top-left plot) and relatively few dances (bottom-left plot), but relatively frequent errors (top-right plot) since only a few bees evaluate the chosen site. High ϵ_q values result in slower decisions, more dancing, and relatively low error rates since many bees evaluate the chosen site. The experimentally-determined quorum threshold value (in the range of 10-20 (Seeley and Visscher, 2003)) is the adaptive result of balancing the trade-off between keeping the median T_a and mean $\sum L_t$ values low and the percent of correct choices high (Passino & Seeley, 2006). This range of ϵ_q also keeps (bottom-right plot) enough bees involved in the process by visiting sites and evaluating them, enough explorers in the role of searching for sites, yet relatively few bees that visit two sites since that can lead to degraded performance in some cases.

5.2 Effect of Initial Dance Strength and Model Validation

For the effect of variation of γ see Figure 7. This shows that the value of 150 waggle runs for the initial dance strength from an excellent site found in experiments (Seeley, 2003) is the result of a trade off between keeping the median T_a and mean $\sum L_t$ values low (high γ values) and the percent of correct choices high (low γ values), while at the same time avoiding split and no-decision cases. This provides a more complete verification that the values used in (Passino & Seeley, 2006) (and here) are in the range settled on by evolution since the class of quality landscapes considered here is considerably broader. Similar results are found for ϵ_s and σ. The results here also help to verify the model in Passino and Seeley (2006) since ϵ_q, ϵ_s, and γ (a parameter not studied in Passino & Seeley, 2006) are the ones found in experiments (Seeley & Buhrman, 1999, 2001; Seeley, 2003; Seeley & Visscher, 2003, 2004a, 2004b).

Overall, from a swarm cognition perspective, the results here show that individual-level bee behavioral parameters related to "early" (γ and ϵ_s) and "late" (ϵ_q) processing (Gazzaniga et al., 1998) have values that are the result of balancing a swarm-level choice speed and accuracy trade-off.

5.3 Effects of Other Behavioral Parameters

Results for considering the tendency to seek to observe dances, $p_m \in [0,1]$ show that this parameter has little effect on most variables. Increasing it does, however, increase the number of split decisions and decrease the number of no-decision cases since there is an increase in coupling in the process that leads to build-up for similar sites to be closer, and helps to ensure that some site will have enough bees to reach a quorum. If site qualities are generated on $[0.2,1]$ but $\epsilon_t \in [0,0.4]$, there is little effect on the choice performance since higher values of ϵ_t simply eliminate inferior alternatives that the swarm is already quite capable of eliminating. Simulations show that all low values of p_d have no major impact on choice performance.

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Figure 6. Effe

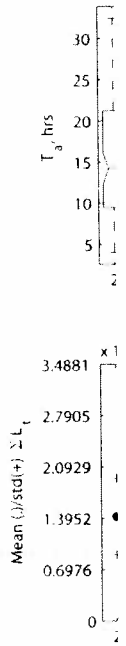

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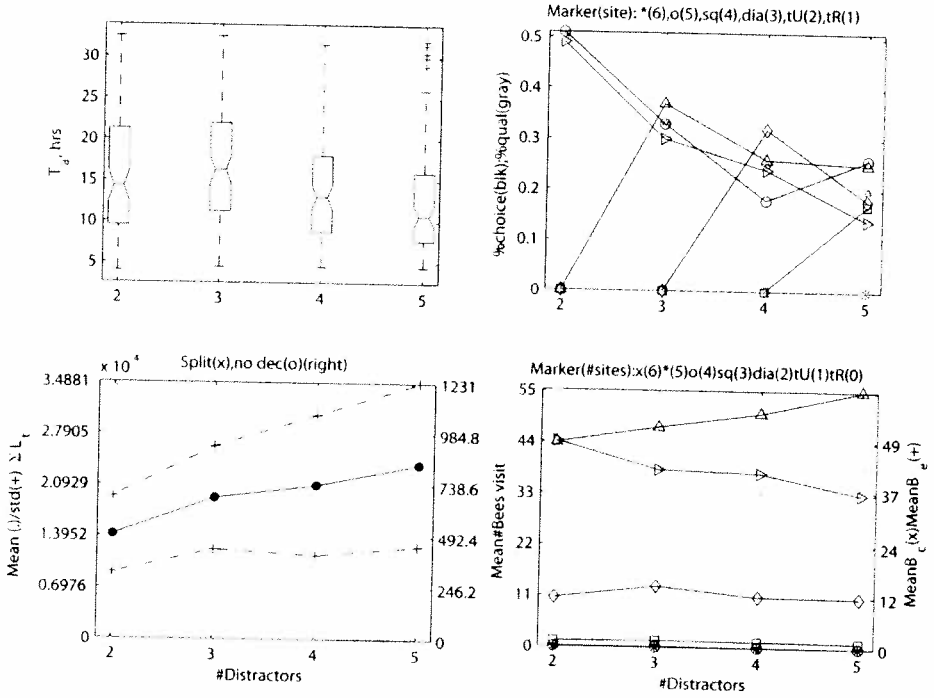
Figure 6. Effect of ϵ_q (see Figure 1 caption for axes explanation)



5.4 Effect of Individual Bee Assessment Noise Magnitude

The effect of varying the magnitude w of the bee assessment noise $w' \in [-w, w]$ is shown in Figure 8. If w increases, the choice error rate does not degrade or improve much over the case where $w = 0.1$, the value from (Passino & Seeley, 2006). It is physiologically impossible for the individual bees to have $w = 0$ and there is little choice performance degradation when w increases to $w = 0.1$. For $w > 0.1$ the choice performance stays nearly the same (and most importantly, does not decrease a lot), but the swarm needs a higher median value of T_a and mean $\sum L_t$ to reach agreement. This is due to a slowing of the decision process due to resolving the differences due to noise. For increasing noise magnitudes, the number of split decisions goes down (since it becomes more unlikely there will be simultaneous agreement) and the number of no-decision cases generally goes up (due to too much confusion caused by the noise). Also, an increasing noise magnitude results in more cross-inhibition as seen in the mean number of bees that visit two sites. This occurs since the noise perturbs the system away from a quick decision and thereby avoids "locking" onto a low quality site. Noise results in more *deliberation* so that on average better sites will be found (i.e., deliberation allows more time for search and consideration).

From a swarm cognition perspective, since group memory is more accurate when more bees are committed to a site (Passino et al., 2008), and choices are made based on group memory, the swarm effectively filters indi-

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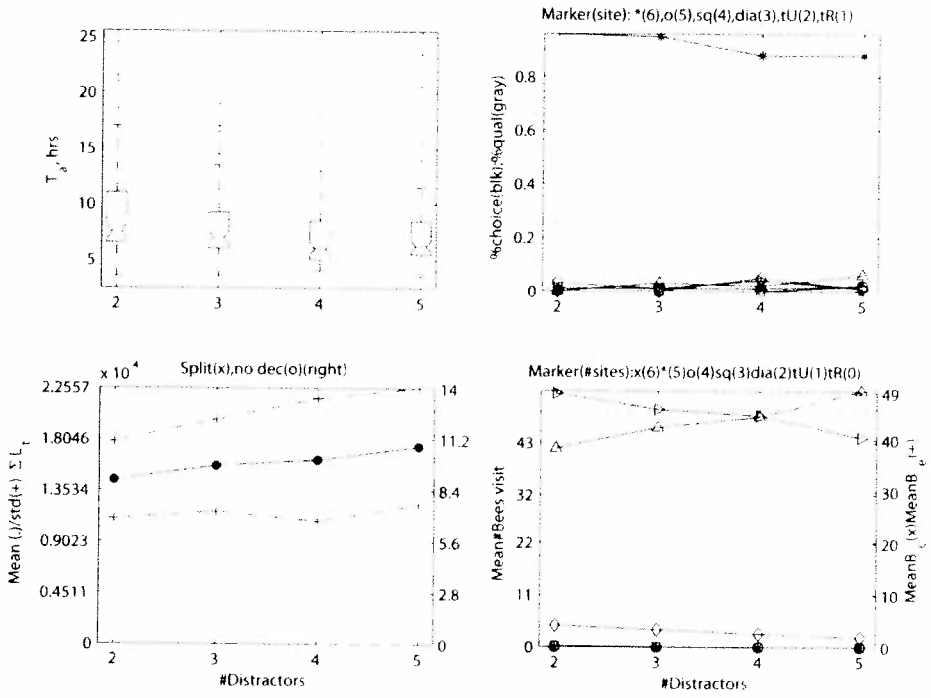
Figure 7. Effect of γ (see Figure 1 caption for axes explanation)



vidual level assessment errors especially for the chosen site (even for unrealistically large quality assessment error magnitudes such as $w = 0.5$). However, natural selection seems to have favored a reduction in individual bee site assessment noise magnitude because that leads to shorter agreement times and less dancing, without much degradation in choice accuracy.

5.5 Effect of Individual Bee Assessment Noise Magnitude on Discrimination

The results in Section 5.4 for the effects of noise magnitude are for a very general class of nest-site quality landscapes. The effect can be amplified for specific and common landscapes. For instance, it seems likely that the swarm will often face discrimination problems for relatively close quality sites. To study the effect of noise magnitude on discrimination, the case of Figure 3 in (Passino et al., 2008) is modified to have all site qualities be zero, except $N^6 = 0.76$ and $N^5 = 0.74$, a differential quality of only 0.02 (which by the results in Figure 3 in (Passino et al., 2008) results in around 50% of the time the swarm choosing each of the two sites). That is, the sites are in the region of generalization and it is difficult for the swarm to discriminate between the two since their quality is so close. Figure 9 shows that by increasing the amount of individual assessment noise, choice performance for the best site stays almost the same as the noise magnitude increases. Notice that in this case 1000 simulations are performed for each parameter value so that at $w = 0.1$ there is about a 5% difference in the choice rates for the two sites. In the region above $w > 0.3$ there is about a 10% difference in the rates of choice for the

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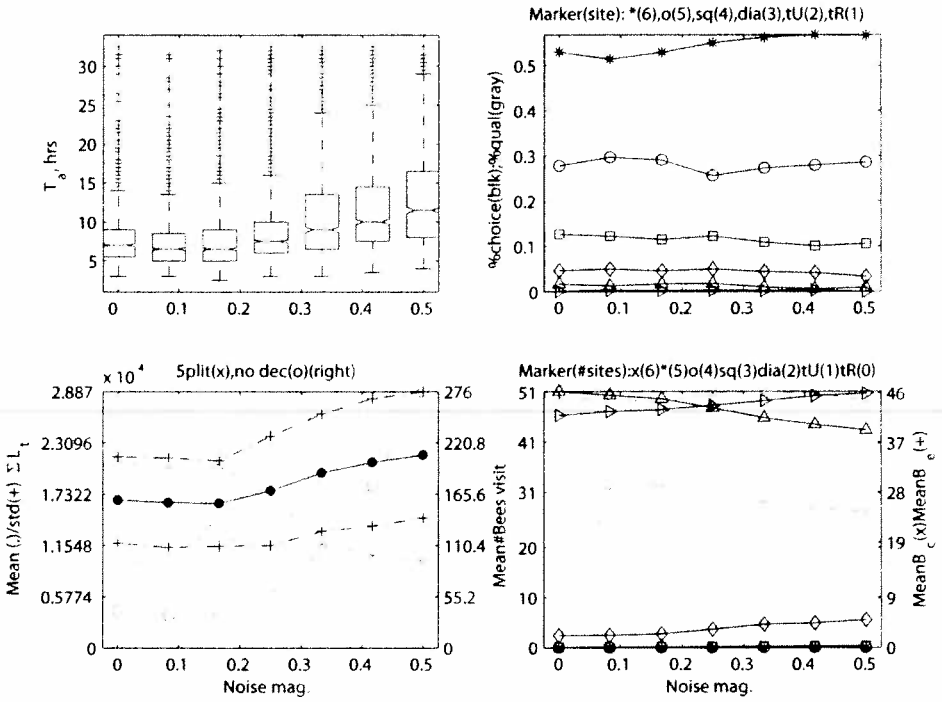
Figure 8. Effect of w (see Figure 1 caption for axes explanation)



two sites; hence, the noise has increased the ability of the swarm discriminate between these close-quality sites. This increase in performance comes, however, at the expense of a higher median T_a and mean $\sum L_t$, and an increased number of no-decision cases. These results further confirm the conclusions reached for the general class of landscapes in the last subsection.

6. CONCLUSION

The swarm choice performance and adaptation studies in this paper provide additional evidence that bee-based swarms have a cognition process that shares key features with neuron-based brains. It was shown that the ability to discriminate depends not only on the differential quality, but also on the absolute quality. In particular, discrimination performance improves for lower quality sites. Next, it was shown that distractors can attenuate the ability of the swarm to discriminate and that discrimination mechanisms try to overcome the negative impacts of distractors. The Treisman feature search test showed that choice performance only degrades slightly if relatively low quality distractors are added to the task of finding the best quality site. The original idea that this provides evidence of parallel processing in the brain clearly also holds for the swarm. Moreover, it was shown that if the high quality site is removed, the swarm takes much longer to decide which site to choose. It was proposed that this was due to a switch in humans to a sequential search mode. Here, however, the delay is clearly induced by the dynamics of the process that leads to deliberation. This provides an alternative way to interpret the delays that occur in reaction time tests, and this may be useful to infer mental dynamics and structure in

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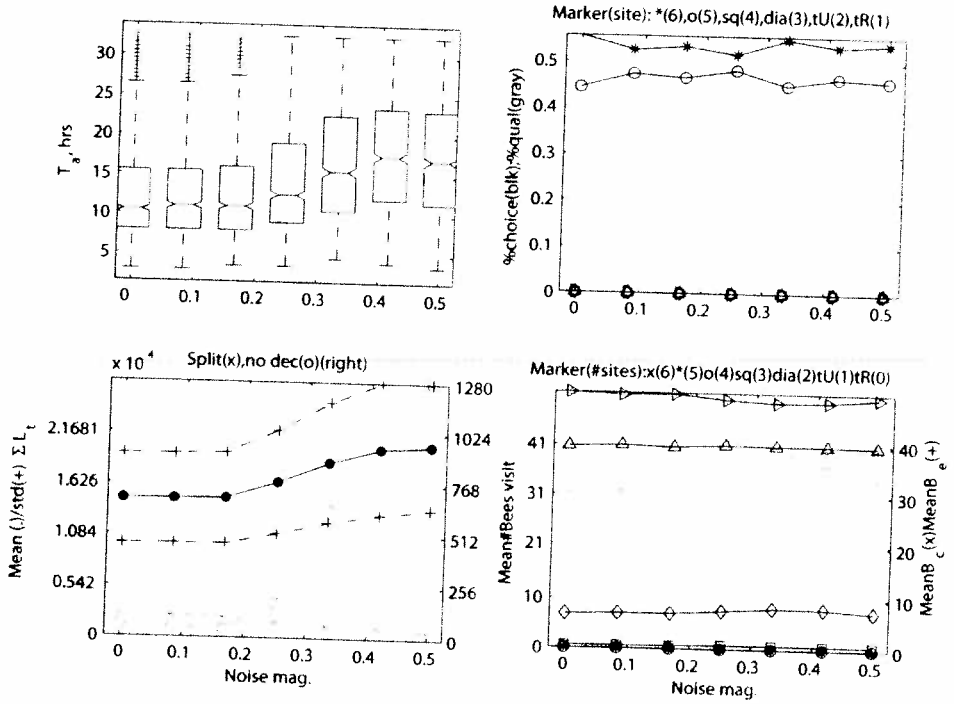
Figure 9. Effect of w, $N^6 = 0.76$ and $N^5 = 0.74$ case (see Figure 1 caption for axes explanation)



other species. The existence of irrational choice behavior commonly found in human decision making in the presence of context-dependent effects was studied. It was shown that for the nest-site selection task, the swarm possesses strong stochastic transitivity and the attraction effect, which both provide evidence that the swarm makes good choices on average. The analysis of the adaptive "tuning" of the processes underlying swarm cognition was a study of the cognitive ecology of the honey bee swarm. It was shown that several behavioral parameters underlying swarm cognition have values evidently shaped by natural selection to balance speed and accuracy of choice. Moreover, it is shown that swarm-level choice performance is insensitive to bee-level assessment errors.

There are a number of directions for future work. First, consideration of the work in (Shafir et al., 2002) on honey bees begs the question if, for the same task and species, context-dependent effects are amplified or attenuated when comparing cases of social and solitary choice. Second, in this paper it was assumed that the number of scouts is $B = 100$. In nature, however, swarms come in different sizes, so that the resulting number of scouts could be in the range $75 \leq B \leq 1000$. It is not known how the size of B and particularly large values of B affect the decision-making process as there have not been experiments conducted to investigate this issue. In fact, it is very difficult to perform such experiments; hence, the investigation of the size of B is likely best done in simulation. This raises a number of questions. For instance, will a larger swarm be more effective at discrimination between the quality

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of two sites? Will it more effectively eliminate distractors from consideration? What will be the effect on context-dependent decision-making? How will the speed-accuracy trade-off be affected? Will a larger size swarm use a higher quorum threshold? Third, it would be useful to conduct a full statistical analysis of the results in this paper (using analysis of variance and the Tukey procedure for multiple comparisons). All these questions await further study.

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