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Negative Incentive Contrast Induces Economic Choice Behavior by Bumble Bees

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A negative incentive contrast experiment was conducted to determine whether responses to a reward reduction facilitate adaptive decisions by bumble bee (*Bombus impatiens*) foragers. In the acquisition phase of the experiment subjects were trained on blue targets (artificial flowers) that contained 50% (weight percent) or 20% sucrose solution and in the test phase subjects were given a choice between familiar targets and yellow targets that had either an economic profitability lower than, equal to, or higher than blue targets, where all targets contained 20% sucrose solution. Subjects trained to a low reward concentration showed a consistent preference for blue targets in the test phase of the experiment, while subjects that experienced a reward reduction exhibited a temporary disruption of consummatory behavior and developed preferences that reflected the profitability of targets. These results support a functional interpretation of responses to a reward reduction: incentive contrast induces foragers to visit alternative sources of nectar and, thereby, facilitates economical decisions. The choice behavior observed over the test phase suggests that associative processes then direct the formation of flower choices.

Many animals, vertebrates and invertebrates, anticipate the magnitude of reward associated with a particular stimulus and exhibit a disruption of consummatory behavior if the expected reward is unrealized (Crespi, 1942; Couvillon & Bitterman, 1984; reviewed by Flaherty, 1982, 1996; Papini, 2003). The adaptive function of behavior observed in incentive contrast studies with food is presumably related to the need of foragers to respond judiciously to spatial or temporal changes of resource quality. The reduction of a reward that is associated with a particular stimulus induces an emotional response that purportedly facilitates a shift from responses that no longer produce an expected reward to responses that are likely to re-establish the successful acquisition of resources (Stout, Muzio, Boughner, & Papini, 2002).

This functional interpretation is supported indirectly by the nearly ubiquitous observation that disrupted consummatory behavior under successive negative contrast recovers relatively rapidly in food-deprived rats, as compared to recovery rates in rats supplied with ample quantities of food (Riley & Dunlap, 1979; see also Dachowski & Brazier, 1991). In addition, the contrast effect is lower in rats that experience a long time interval between their final experience with the larger reward and their initial experience with the lower reward (Gordon, Flaherty, & Riley, 1973; Ciszewski & Flaherty, 1977). The disruption of consummatory behav-

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ior induced by a reward reduction also recurs under conditions of repeated reward shifts, which suggests that individuals continually adjust reward expectations with experience (Flaherty, Becker, & Checke, 1983). These observations are consistent with general properties of rewards in nature, namely that their value depends on individual status and their reliability deteriorates with the duration of the time interval between encounters with a particular stimulus.

However, the adaptive function, or survival value, of behavioral responses to reward shifts per se has yet to be firmly established. Indeed, the emotional component of responses to reward reductions may induce irrational behavior, or other seemingly non-adaptive physiological responses (Archer, 2001; but see Papini, 2003). The adaptive function of behavior is inferred from the *causal* relationship between behavior and fitness or by use of the comparative method (Tinbergen, 1963, 1989; Hailman, 1976). Thus, the adaptive function of a response to reward reduction can be inferred from an experiment in which a contrast effect induces a gain in some currency related to fitness, relative to the fitness returns to individuals whose behavior is not disrupted by the magnitude of the reduced reward.

In this study, we used this experimental approach to investigate the potential adaptive function of behavioral responses of bumble bee (*Bombus impatiens*) foragers to a reduction of nectar concentration in flowers. In particular, we used a successive negative incentive contrast experimental design to motivate foragers to shift from a familiar target (artificial flower) to unfamiliar, alternative targets that had an economic profitability lower than, equal to, or higher than the economic profitability of familiar targets. The choice behavior of these subjects was compared to the behavior of subjects that experienced a consistent low level of reward. The patterns of choice behavior we observed indicate that responses to a reward reduction indeed facilitate economical choices by foragers. Incentive contrast induces foragers to visit alternative flowers and associative processes appear to shape the development of economical flower preferences.

The goal of this study was to determine whether incentive contrast effects facilitate adaptive decisions by bumble bee foragers, where net energy gain per flower served as the fitness currency (Stephens & Krebs, 1986). The methods we used follow a simple modification of a successive negative contrast experimental design (see Eisenberger, Frank, & Park, 1975; Wiegmann, Wiegmann, & Waldron, 2003).

In the acquisition phase of our experiment subjects in downshift groups were trained on targets—artificial flowers—that had an intermediate cost to handle (and delay to reward) and an associated high concentration sucrose solution reward. The concentration of sucrose solution in these targets was then downshifted in a test phase and subjects were given a choice between familiar targets and alternative targets that had either a lesser, equal, or higher cost to handle (and delay to reward) relative to the familiar target, where all targets contained an equal volume of low concentration of sucrose solution. The alternative targets were not presented until the test phase of the experiment, a procedure designed to prohibit the devaluation of these stimuli in the acquisition phase (Spear & Spitzer, 1969; see Eisenberger et al., 1975). The behavior of these subjects was compared to the behavior of subjects in control groups that experienced a low concentration of sucrose solution in all targets throughout the experiment.

Method

Subjects and Pretraining

Bumble bees (*B. impatiens*) were obtained from Koppert Biological Systems, Romulus, Michigan. Subjects were trained to targets positioned in an enclosed 82 x 41 x 41 cm clear plastic test arena connected to the colony by a 41 x 41 x 41 cm flight arena. Subjects entered the test arena through a 10 x 10 cm window, which allowed us to restrict access to the arena to a single individual. Targets were elevated on a platform (positioned to the height of the window) located 115 cm from the colony.

Subjects were pre-trained to 2-cm, 8-cm, and 14-cm clear plastic, tubular targets (two of each type) filled with 20% (weight percent) sucrose solution. Green electrical tape was placed around the perimeter of the top of each tube and the inside of each tube was scratched to provide traction. Individuals that learned to extract sucrose solution from these targets were marked on the thorax with colored lacquer paint for individual identification.

Procedure

The experiment involved 96 subjects, divided equally into three downshift groups and three control groups. Subjects in downshift groups were trained in an acquisition phase of 20 sessions—which began when a subject flew into the test arena and ended when she exited the arena to unload the extracted sucrose solution at the colony—on a cluster of four 8-cm blue targets (i.e., 8-cm clear plastic tubes marked with blue electrical tape) that contained 50% sucrose solution in a well at the base of each flower. These subjects were then given a choice between four clustered blue targets and four clustered yellow targets in a test phase of 20 sessions, where all targets contained an equal volume of 20% sucrose solution. Subjects were not allowed to exit the test arena in any session until they had imbibed all of the sucrose solution from at least one target, but the movement of subjects to and from the colony otherwise determined session durations and inter-session intervals. Subjects in control groups were trained identically, except that blue targets contained 20% sucrose solution in each phase of the experiment.

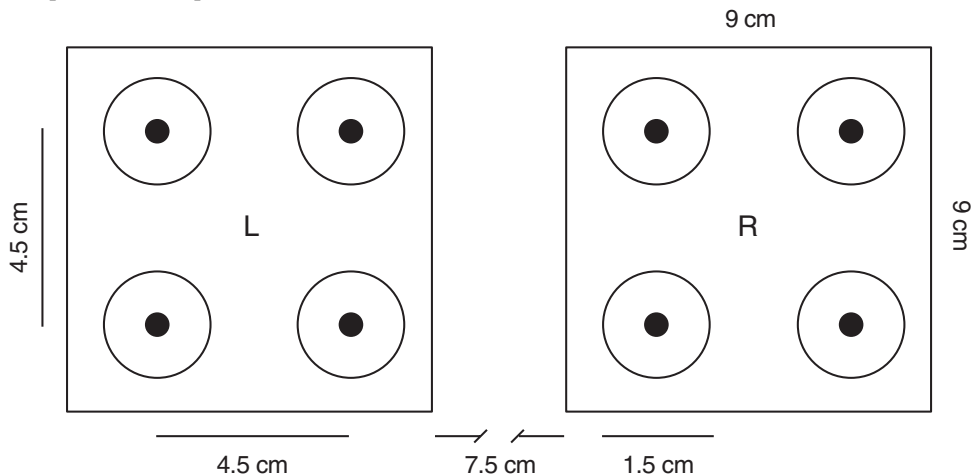


Figure 1. Targets used in the experiment, with dimensions of target diameters and inter-target distances. Target depth was visible to subjects.

In the acquisition phase of the experiment targets were each initially filled with 25 μ L of sucrose solution. The volume of solution in each target was increased by 5 μ L if a subject extracted all of the available sucrose solution from each target three consecutive sessions. This procedure ensured that subjects visited multiple targets in each session and that they were not forced to visit more than one target type in the test phase of the experiment. The blue targets were alternated between two positions—R and L—on the platform in the pseudo-random sequence R, L, L, R, L, R, R, L, ..., L, R, R, L or L, R, R, L, R, L, L, R, ..., R, L, L, R to prevent the development of site preferences (Figure 1; Shafir, Wiegmann, Smith, & Real, 1999; see also Kells & Goulson, 2001). This pattern continued

over the test phase of the experiment, where the cluster of yellow targets was positioned in the location not occupied by blue targets. The flower tubes and nectar wells were replaced after each session to prevent any influence of scent marks on choice behavior (Gilbert et al., 2001).

Table 1
The Characteristics of Blue (B) and Yellow (Y) Targets Encountered by (Downshift) Subjects that Experienced a Downshift of Reward Between the Acquisition and Test Phases of the Experiment and (control) Subjects that Experienced a Constant Concentration of Sucrose Solution in Targets.

		Sessions						
		Acquisition Phase			Test Phase			
		[Sucrose]	Depth (cm)		[Sucrose]	Depth (cm)		
Group	Treatment	N	B	B	B	Y	B	Y
8-2	Downshift	16	50%	8	20%	20%	8	2
	Control	16	20%	8	20%	20%	8	2
8-8	Downshift	16	50%	8	20%	20%	8	8
	Control	16	20%	8	20%	20%	8	8
8-14	Downshift	16	50%	8	20%	20%	8	14
	Control	16	20%	8	20%	20%	8	14

The yellow targets presented in the test phase of the experiment varied in profitability, the net energy gained per unit of handling time (Table 1; Stephens & Krebs, 1986; see Cheng, Pena, Porter, & Irwin, 2002; Shafir, Waite, & Smith, 2002.). Subjects in Group 8-2 were given a choice between four 8-cm blue targets and four 2-cm yellow targets, where all targets contained 20% sucrose solution. Likewise, subjects in Group 8-8 and Group 8-14 were given a choice between four 8-cm blue targets and four 8-cm and four 14-cm yellow targets, respectively. Otherwise, subjects in each group were treated identically. We recorded which targets were visited by subjects in each session, where a visit was specified by the entrance of a subject into a flower tube and proboscis insertion (one or more times) into its nectar well. The duration of each session and inter-session intervals were measured to the nearest second.

Preliminary Study

A preliminary test was conducted to ensure that bumble bees prefer relatively shallow targets in the context of our experimental design and to determine whether the colors of stimuli used in our experiment impede the development of economical preferences. Subjects were trained on four clustered blue and four clustered yellow targets filled with 20% sucrose solution presented alternatively in 12 sessions. Subjects were then given a choice between four blue targets and four yellow targets presented simultaneously in 12 test sessions, where all targets contained an equal volume of 20% sucrose solution. Titration of reward volumes and the movement of targets followed the procedures described earlier. Six subjects were given a choice between 2-cm targets and 8-cm targets, where stimulus color was counterbalanced with the depth of targets. Likewise, six subjects were given a choice between 8-cm and 14-cm targets.

Subjects preferred the shallower, more economically profitable target in test sessions, regardless of its color. Indeed, 11 of the 12 subjects visited shallower targets more frequently than the

more costly alternative targets. A Sign test indicates that this proportion deviates significantly from the null expectation that subjects are indifferent to target profitability, $s = 11$, $p = 0.004$. Subjects trained on 2-cm and 8-cm artificial flowers chose 2-cm targets in $\theta \pm \text{SE} = 0.78 \pm 0.05$ of all visits to targets in test sessions. A one-tailed, one sample Student's t test indicates that this preference is significantly higher than the chance expectation of $\theta = 0.5$, $t(5) = 5.17$, $p = 0.0018$. Likewise, subjects trained on targets with depths of 8-cm and 14-cm chose the 8-cm target in more than half (0.62 ± 0.05) of all visits to targets in the test sessions, $t(5) = 2.28$, $p = 0.0357$.

Results

Consummatory Behavior

Figure 2 shows the number of targets visited by subjects over the acquisition sessions, the initial test session and postdownshift test sessions. A repeated-measures analysis of variance (ANOVA) indicates a significant main effect for treatment, $F(1, 90) = 210.06$, $p < 0.0001$, and session, $F(2, 180) = 208.62$, $p < 0.0001$, and a significant interaction between these factors, $F(2, 180) = 207.28$, $p < 0.0001$. Repeated measures ANOVA for session durations and intersession intervals similarly reveal significant main effects for treatment, $F(1, 90) = 257.64$, $p < 0.0001$ and $F(1, 90) = 26.99$, $p < 0.0001$, and session, $F(2, 180) = 217.76$, $p < 0.0001$ and $F(2, 180) = 8.35$, $p = 0.0003$, and a significant interaction between these factors, $F(2, 180) = 231.17$, $p < 0.0001$ and $F(2, 180) = 11.34$, $p < 0.0001$ (Figure 3). Thus, these measures of consummatory behavior for subjects in Groups 8-2, 8-8, and 8-14 varied similarly across sessions, but responses depended on the initial reward concentration in blue targets.

In the acquisition phase of the experiment subjects in downshift groups made $\bar{x} \pm \text{SE} = 3.58 \pm 0.04$ visits to targets per session, with a mean session duration and inter-session interval of 154.49 ± 3.25 seconds and 63.76 ± 1.98 seconds, respectively. Subjects in control groups made 3.32 ± 0.08 visits to targets per session in the acquisition phase of the experiment, with a mean session duration and inter-session interval of 122.71 ± 2.58 and 49.71 ± 1.55 seconds. A Fisher's protected least significant difference (Fisher's PLSD) posthoc comparison of these means indicates that neither the numbers of visits to targets, $t(90) = 0.19$, the durations of sessions, $t(90) = 0.80$, nor the mean inter-session intervals, $t(90) = 1.06$, differed between these subjects.

In the initial session of the test phase—the session in which subjects in downshift groups first experienced a reduced reward—subjects that experienced a downshift of reward exhibited a severe disruption of consummatory behavior relative to subjects that experienced a consistent low level of reward. Subjects that experienced a reward reduction visited and rejected the reward offered in blue and yellow targets repeatedly and they made an average of 22.90 ± 1.36 visits to targets, significantly more visits than the 3.44 ± 0.12 visits made by subjects that experienced a consistent level of reward, Fisher's PLSD $t(90) = 101.23$, $p < 0.0001$. The disruption of consummatory behavior was also evident in the duration of the initial test session and the intersession interval that followed this session. The duration of the initial test session for subjects that experienced a downshift of reward was 708.58 ± 39.46 seconds and the pursuant intersession interval was 92.51 ± 11.18 seconds. In contrast, the duration of the initial test session and the intersession interval for subjects in control groups were 105.73 ± 3.00 seconds and 46.54 ± 1.55 seconds, respectively. A Fisher's PLSD posthoc comparison indicates

that session duration, $t(90) = 15.91$, $p < 0.0001$, and the intersession interval, $t(90) = 3.46$, $p = 0.0008$, differed between subjects in these two groups.

The effect of the reward downshift on consummatory behavior was transitory and the consummatory behavior of subjects in Groups 8-2, 8-8 and 8-14 was similar in subsequent sessions of the test phase of the experiment, regardless of the initial reward concentration in blue targets. A Fisher's PLSD comparison indicates that neither the mean number of targets visited by subjects, $t(90) = 0.14$, the mean session duration, $t(90) = 0.06$, nor the mean inter-session interval, $t(90) = 0.34$, differed between subjects in downshift and control groups in test sessions after the initial session in the test phase of the experiment.

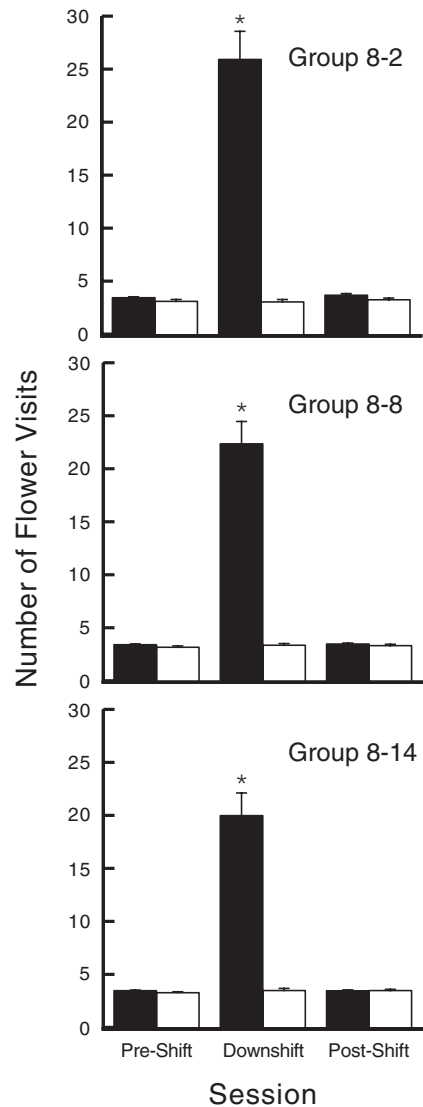


Figure 2. Number of target visits ($\bar{X} + SE$) in the (preshift) acquisition phase, the initial (downshift) session of the test phase and the remainder of the (postshift) test sessions for subjects that (solid bars) experienced a downshift of reward and (open bars) subjects that experienced a constant concentration of sucrose solution in blue targets. Significant Fisher's PLSD posthoc tests for differences of means at $\alpha = 0.05$ are indicated by an asterisk.

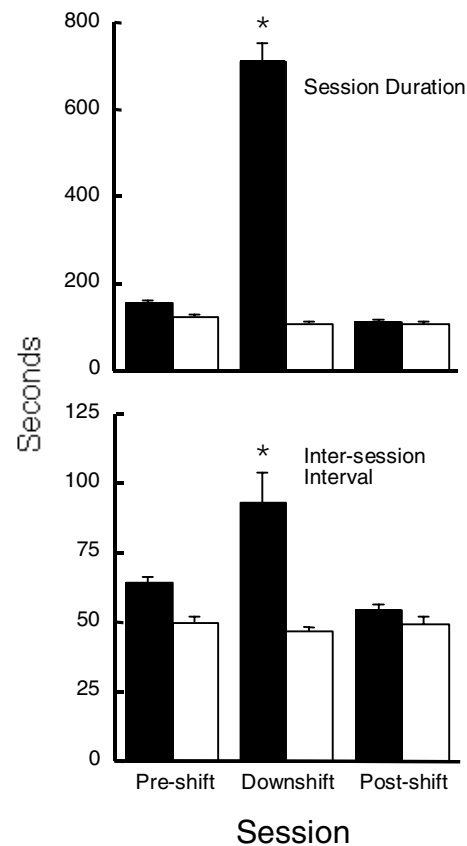


Figure 3. Session durations and inter-session intervals ($\bar{X} + SE$) in the (preshift) acquisition phase, the initial (downshift) session of the test phase and the remainder of the (postshift) test sessions for subjects that (solid bars) experienced a downshift of reward and (open bars) subjects that experienced a constant concentration of sucrose solution in blue targets. Significant Fisher's PLSD posthoc tests for differences of means at $\alpha = 0.05$ are indicated by an asterisk.

Choice Behavior

The choice behavior of subjects was affected by the downshift of reward and the relative profitability of yellow targets. In the initial session of the test phase the first target visited by every subject was invariably blue and subjects in control groups visited blue targets nearly exclusively in this session. A two-way ANOVA of these proportions (angular transformed to stabilize the variance of responses) indicates that the target preferences differed significantly amongst subjects in Groups 8-2, 8-8 and 8-14, $F(2, 90) = 7.01, p = 0.0015$, a significant influence of treatment, $F(1, 90) = 44.348, p < 0.0001$, and a significant interaction between these two factors, $F(2, 90) = 3.15, p = 0.0337$. Subjects in Group 8-14 visited a similar proportion of blue targets, regardless of the initial concentration of reward in these targets, Fisher's PLSD $t(90) = 1.87$, while subjects in Groups 8-2 and 8-8 that experienced a reward reduction visited a significantly lower proportion of blue targets than subjects in respective control groups (Figure 4). Subjects in Group 8-14 that experienced a reward reduction also visited a higher proportion

of blue targets than subjects that experienced a downshift of reward in Group 8-2, Fisher's PLSD $t(90) = 3.30$, $p = 0.0014$, or Group 8-8, Fisher's PLSD $t(90) = 4.19$, $p < 0.0001$. The choice behavior of subjects in Groups 8-2 and 8-8 that experienced a downshift of reward was similar, Fisher's PLSD $t(90) = 0.89$.

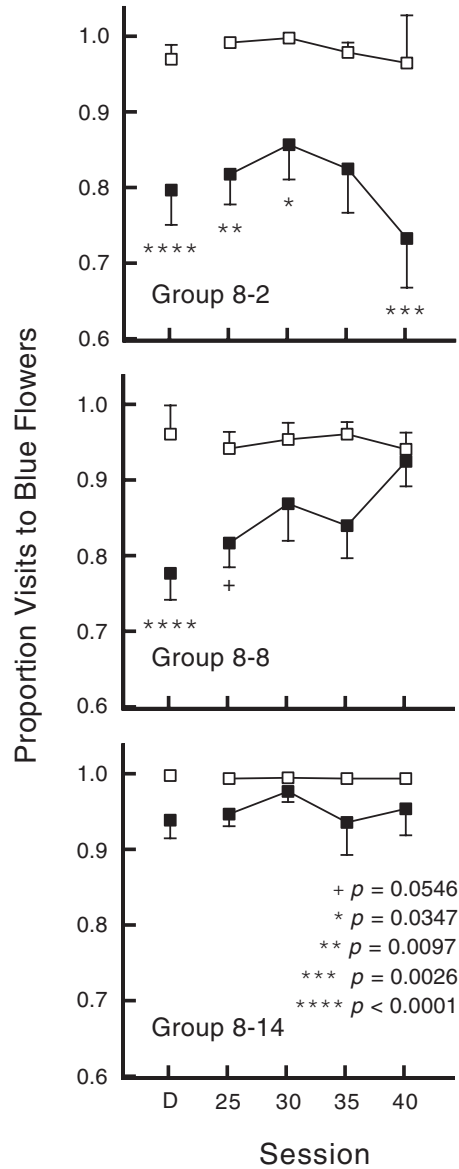


Figure 4. Visits to blue targets by subjects over (blocks of five) test sessions. The proportion of visits to blue targets by subjects in the initial (downshift) test session (D) are shown to the left of the series. Proportions ($\theta - SE$) for subjects that experienced a reward downshift are indicated by solid squares and proportions ($\theta + SE$) for subjects that served as controls are indicated by open squares. The probabilities shown correspond to Fisher's PLSD post-hoc comparisons of (angular transformed) proportions.

The similarity of choice behavior between subjects in Group 8-14 in the initial test session is attributable in part to the relatively weak influence of the reward reduction on the likelihood that subjects visited yellow targets. A total of 11, 14 and 5 of the 16 subjects in Groups 8-2, 8-8 and 8-14 that experienced a downshift of reward visited a yellow target at least once in the initial test session. A chi square test indicates that these proportions differ significantly, $X_2^2 = 11.20$, $p = 0.0037$, and a Tukey-like pairwise test reveals that subjects in Group 8-14 were less likely to visit a yellow target than subjects in Group 8-8, $q(3) = 4.67$, $p < 0.005$.

The similarity of choice behavior between subjects in Group 8-14 in the initial test session is also attributable to the disinclination of subjects to revisit yellow targets. The proportion of revisits to yellow targets by subjects in Groups 8-2, 8-8 and 8-14 that experienced a downshift of reward—and visited at least one additional target after an initial visit to a yellow target—was 0.59 ± 0.09 , 0.31 ± 0.04 and 0.25 ± 0.08 , respectively. A one-way ANOVA indicates that the proportion of revisits to yellow targets depended on the depth of yellow targets, $F(2, 25) = 5.68$, $p = 0.0093$. Fisher's PLSD post-hoc comparisons indicate that subjects in Group 8-2 revisited a higher proportion of yellow targets than did subjects in Group 8-8, $t(25) = 2.80$, $p = 0.0098$, or Group 8-14, $t(25) = 2.66$, $p = 0.0135$. The proportion of revisits to yellow targets did not differ between subjects in Groups 8-8 or 8-14, $t(25) = 0.53$.

The reward reduction experienced by subjects in downshift groups in the initial test session had a less transitory effect on choice behavior than on consummatory behavior, but the development of target preferences over the test phase depended on the relative profitability of targets (Table 2). Figure 4 reveals that subjects in control groups visited a consistent, high proportion of blue targets over the entire test phase of the experiment. Indeed, all subjects showed a preference for blue targets throughout the test phase of the experiment. However, subjects in Group 8-2 that experienced a downshift of reward showed a gradual decline in the proportion of visits to blue targets and they visited the more economical yellow targets significantly more frequently than subjects in the control group over most of the test sessions. Subjects in Group 8-8 that experienced a downshift of reward visited blue targets less frequently than subjects in the control group in the initial test session, but the proportion of blue targets visited by these subjects *increased* to the level of subjects in the control group over the remainder of the test sessions. The choice behavior of subjects in Group 8-14 that experienced a downshift of reward remained similar to the behavior of subjects in the control group over the entire test phase of the experiment.

Discussion

In this study, we used a negative incentive contrast design to determine whether incentive contrast effects promote adaptive flower choices by bumble bee foragers. Subjects that experienced a downshift of reward in familiar targets showed a severe disruption of consummatory behavior, a behavioral response observed in earlier incentive contrast studies of hymenopterans (Bitterman, 1976; Couvillon & Bitterman, 1984; Wiegmann et al., 2003). Furthermore, these subjects were relatively likely to visit the alternative, novel target in the initial session of the test phase than subjects that experienced a consistent low reward, a result that

also parallels observations of other animals tested under analogous experimental conditions (reviewed by Eisenberger et al., 1975; see also Greggers & Menzel, 1993; Keasar, Shmida, & Motro, 1996). The choice behavior of bumble bee foragers appears to be similarly affected by deviations from reward expectations under natural conditions. For example, bumble bees are more likely to visit alternative flowers after a relatively short visit—an encounter with an unusually low, unexpected volume of nectar—to a particular flower (Chittka, Gumbert, & Kunze, 1997). This contrast effect in the context of our experiment facilitated the development of economical choices, which supports the hypothesis that responses to reward reduction are evolutionary adaptations to enhance the acquisition of resources.

Table 2
Repeated Measures ANOVA for (Angular-transformed) Proportions of Blue Targets Visited Over (Blocks of Five) Sessions of the Test Phase.

Source	<i>df</i>	Sum of Squares	Mean Square	<i>F</i>	<i>p</i>
Group	2	5503.05	2751.52	6.18	0.0031
Treatment	1	11035.62	11035.62	24.77	<0.0001
Group x Treatment	2	3068.49	1534.24	3.44	0.0362
Subject (Group)	90	40096.50	445.52		
Session	3	710.18	236.73	4.20	0.0064
Session x Group	6	865.44	144.24	2.56	0.0200
Session x Treatment	3	368.39	122.80	2.18	0.0911
Session x Group x Treatment	6	822.27	137.05	2.43	0.0265
Session x Subject (Group)	270	15234.64	56.43		

In the initial session of the test phase of our experiment subjects that experienced a reward reduction visited and rejected blue *and* yellow targets. This result is consistent with the idea that foragers form patch-level expectations of reward in addition to flower-specific reward expectations (Greggers & Menzel, 1993; Greggers & Mauelshagen, 1997; Wiegmann et al., 2003). The effect of the reward reduction on consummatory behavior observed in this study was transient, as repeated visits to targets presumably caused foragers to alter their reward expectations (see Couvillon & Bitterman, 1991). Indeed, the reactions of foragers to the low concentration of sucrose solution in post-downshift sessions of the test phase mirrored the pre-downshift responses in the acquisition phase of the experiment.

The influence of the economic profitability of yellow targets on the formation of target preferences was also evident in the first session of the test phase of

the experiment. Subjects in Group 8-2 encountered yellow targets that had a higher profitability than familiar blue targets and subjects that experienced a downshift of reward revisited yellow targets more often than subjects in Group 8-8 or Group 8-14. In subsequent test sessions these subjects showed a gradual decrease in their visitation rate to blue targets and they visited a lower proportion of blue targets over most of the test phase than subjects in the control group that did not experience a downshift of reward. Subjects in Group 8-14 encountered yellow targets that had a lower profitability than familiar blue targets and subjects in this group that experienced a downshift of reward, like subjects in the control group, rarely visited yellow targets.

The pattern of flower choice exhibited by subjects in Group 8-8, in combination with these observations, reveals the likely mechanism that underlies the formation of flower preferences. Subjects in Group 8-8 encountered yellow targets that had a profitability equal to familiar blue targets and, in the initial test session, subjects that experienced a reward reduction visited a relatively high proportion of yellow targets. However, the proportion of blue targets visited by these subjects *increased* over the test phase of the experiment and, ultimately, their target choices did not differ from the choices of subjects that experienced no downshift of reward. This pattern of choice behavior, in particular, suggests that, if expectations of reward are unrealized, associative processes modulate the formation of flower choices.

The behavior of subjects in Group 8-8 is inconsistent with a non-associative cognitive process, as a perfectly rational forager would have visited blue and yellow targets equally frequently. Instead, the extensive history of reinforcement on blue targets appears to have dominated choice behavior. In addition, the transition of target choices by subjects in Group 8-2 to yellow targets was gradual, rather than abrupt, as is characteristic of associative processes. Subjects in Group 8-14 also exhibited behavior consistent with associative processes, but their behavior is less informative of the cognitive mechanism that underlies the formation of flower preferences because the economics of target choice and reinforcement history each favored specialization on blue targets. Studies of frequency-dependent flower choice in bumble bees similarly reveal the influence of associative processes in the formation of flower preferences (reviewed by Smithson, 2001; see also Goulson, 1994; Keusar, Bilu, Motro, & Shmida, 1997; Smithson & Macnair, 1997; Menzel, 2001).

The flower choices of bumble bee foragers certainly also involve other psychological processes (Dukas & Waser, 1994; Wiegmann, Wiegmann, MacNeal, & Gafford, 2000; reviewed by Menzel & Giurfa, 2001). In this experiment the numbers of subjects in each group that visited yellow targets in the initial test session suggest, for example, that attributes of blue targets were generalized (see also Waser, 1986; Laverty, 1994; Wilson & Stine, 1996). Subjects in Group 8-8 experienced alternative targets that differed in only one dimension, namely color, from familiar blue targets—whereas the alternative targets presented to subjects in Groups 8-2 and 8-14 differed from familiar targets in both depth and color—and subjects in this group were relatively likely to visit yellow targets. Indeed, variability within and between flower characteristics, and hence generalization, is likely to influence the diversity of flowers visited by a forager (Gumbert, 2000; reviewed by Geger & Laverty, 2001). Morphological similarities between flowers may also

allow for positive transfer of techniques used to handle familiar flowers to novel, alternative flowers (Lavery, 1994; Chittka & Thomson, 1997). The likelihood that subjects visited yellow targets in the initial session of the test phase of the experiment may also have been influenced by experiences with the green targets—which had depths equivalent to yellow targets—used to pre-train individuals.

The behavior of bumble bees in our study suggests that incentive contrast effects and associative processes influence the development and persistence of flower choices. The results of our experiment support a functional interpretation of responses to a reward reduction: incentive contrast induces foragers to visit alternative flowers and, thereby, facilitates economical decisions. Initial experiences with alternative flowers and earlier experiences with familiar flowers influence short-term behavior, which is then directed toward the formation of economical flower choices by associative processes.

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