

Sharoni Shafir · Tom A. Waite · Brian H. Smith

Context-dependent violations of rational choice in honeybees (*Apis mellifera*) and gray jays (*Perisoreus canadensis*)

Received: 22 May 2001 / Revised: 1 September 2001 / Accepted: 6 September 2001 / Published online: 19 October 2001
© Springer-Verlag 2001

Abstract Contrary to the theory of rational choice, adding an alternative to a set of available options often affects people's judgement of the preexisting options. Here, we show that honeybees (*Apis mellifera*) and gray jays (*Perisoreus canadensis*) are also influenced by the addition of an option to a choice set (i.e., by a change in local context). Like humans, our subjects violated basic properties of rational choice. Their relative preference between two original options changed with the introduction of a third, relatively unattractive option. Such context-dependent choice violates the constant-ratio rule. Our subjects increased their *relative* preference for the more similar of two alternatives, contrary to the similarity hypothesis. The jays also increased their *absolute* preference for the more similar of two alternatives, in violation of regularity. Thus, the principle of irrelevant alternatives, which assumes that preference between options does not depend on the presence or absence of other options, is violated not only by humans, but also by an invertebrate and a nonhuman vertebrate. These findings contradict the view that nonhuman animals should be immune to such psychological effects and that they should conform with normative accounts, such as rationality or optimal-foraging theory, because their decision-making processes are evolutionarily adaptive. We discuss the potential generality of context-dependent

effects and suggest that such effects should be incorporated into decision-making models in behavioral ecology.

Keywords Asymmetric dominance · Context-dependent preferences · Foraging · Rationality · Regularity · Honeybees · Gray jays

Introduction

It is tempting to assume that animals evaluate options independently, such that the value assigned to a particular option is not affected by the presence or absence of other options. This assumption is often incorporated into models in a variety of disciplines, including economics, psychology, and behavioral ecology (see Tversky and Simonson 1993; Shafir 1994). Rationality theory can be seen as a collection of compelling principles that are formalized into theories of decision and choice (Shafir 1993; Doyle et al. 1999). While usually applied as a normative theory for humans (i.e., what the idealized human *should* do), similar principles are often extended to animals, as in optimal-foraging theory (Stephens and Krebs 1986). A fundamental aspect of rationality theory (and optimal-foraging theory) is that options have fixed values (but see Houston 1997). This notion, however, is systematically violated in studies where humans evaluate options in a context-dependent manner, where the context refers to the alternatives that comprise the choice set (Payne et al. 1992, 1999; Tversky and Simonson 1993; Doyle et al. 1999; Sedikides et al. 1999). Several recent studies reveal that context-dependent choice may also be common in nonhuman animals (Shafir 1994; Hurly and Oseen 1999; Wiegmann et al. 2000; Waite 2001a, 2001b).

An intuitive consequence of assigning independent (absolute) values to options is that they should be ranked in a transitive manner by the decision-maker. That is, if A is preferred to B, and B is preferred to C, then A is preferred to C. Finding violations of transitive choice patterns, therefore, both in humans (Tversky 1969) and

Communicated by H. Kokko

S. Shafir (✉) · B.H. Smith
Department of Entomology, The Ohio State University,
1735 Neil Avenue, Columbus, OH 43210-1220, USA

T.A. Waite
Department of Evolution, Ecology, and Organismal Biology,
The Ohio State University, 1735 Neil Avenue, Columbus,
OH 43210-1293, USA

Present address:

S. Shafir, B. Triwaks Bee Research Center and Department
of Entomology, The Hebrew University of Jerusalem,
Rehovot 76100, Israel
e-mail: shafir@agri.huji.ac.il
Tel.: +972-8-9489401, Fax: +972-8-9466768

in nonhuman animals (Navarick and Fantino 1972; Shafir 1994; Waite 2001a), suggests that options are not assigned fixed values, but rather that choice is context dependent. In other words, choice does not merely reflect the subjective evaluation of independent attributes of options, but is influenced by the characteristics of the other options that are being compared.

Context effects in human choice behavior have also been studied by comparing subjects' preferences between two options when presented alone and when presented along with a third alternative (Huber et al. 1982; Huber and Puto 1983; Simonson 1989; Simonson and Tversky 1992; Shafir et al. 1993; Tversky and Simonson 1993; Doyle et al. 1999; Sedikides et al. 1999). For the aggregate data of a group of respondents, or the multiple responses of subjects, absolute preference of a particular option is determined by the number of choices of that option divided by the total number of choices. Relative preference between two options is the number of choices of one option divided by the total number of choices of the two options. In the framework of the option set depicted in Fig. 1, for example, the preference of the target (T) relative to the competitor (C), is equal to the proportion choice of T divided by the sum of proportion choice T and proportion choice C.

Binary choice is a special case in which the denominator equals 1, and the preference of T relative to C is equal to the absolute proportion choice of T. In the case of three (or more) options, relative preferences between any two options are still computed as above. If options have fixed values, then according to the constant-ratio rule (Luce 1959; Tversky 1972), the relative preference between two options is independent of the presence or absence of other options that may be added to the choice set. Therefore, the preference of T relative to C in the binary case is equal to the preference of T relative to C in the trinary (or more) case.

The constant-ratio rule is consistently violated in human studies: the relative preference between options is *often* affected by the presence of other options (Tversky 1972; Luce 1977; Payne et al. 1992, 1999; Tversky and Simonson 1993; Doyle et al. 1999; Sedikides et al. 1999). Models have been developed that could account for this context dependence. According to a compelling alternative to the constant-ratio rule, the similarity hypothesis (Tversky 1972), a third option competes more with the option that is most similar to it. In the framework of Fig. 1, the target loses more than the competitor from the introduction of the decoy, so the relative preference of T over C decreases when D is introduced (see Tversky and Simonson 1993 for a more formal discussion).

In a particular construction of the three-option set, the decoy is asymmetrically dominated (Fig. 1). An option that is clearly less attractive than an alternative is said to be dominated by it. In the asymmetric dominance construction, the decoy is dominated by the target but not by the competitor. This asymmetry may cause the target, which is more similar to the decoy than the competitor, to lose less than the competitor from the introduction of

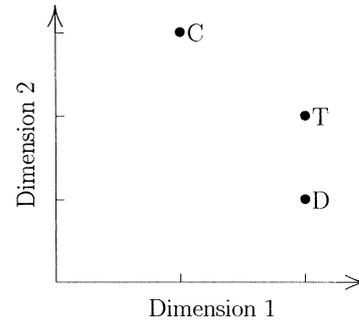


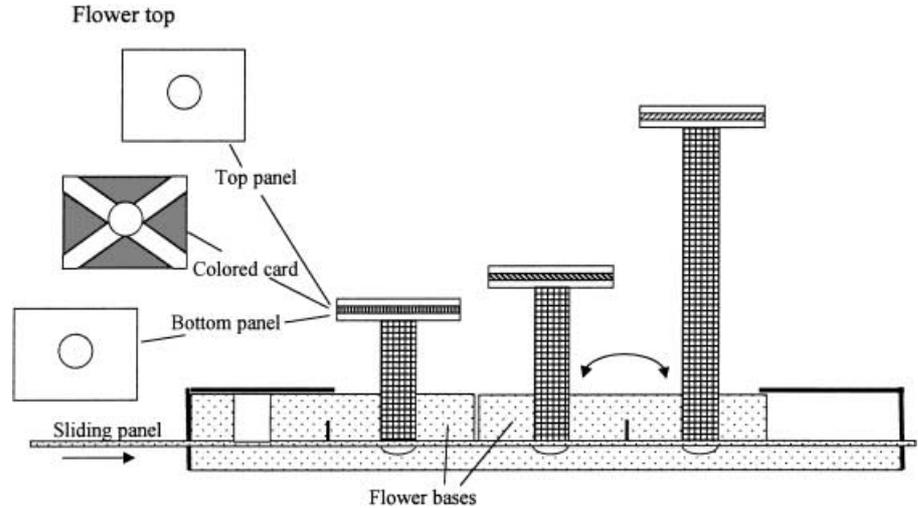
Fig. 1 Schematic representation of the attributes of three options in tests of the asymmetric dominance effect. The target (T) is more attractive than the competitor (C) along dimension 1 but is less attractive along dimension 2. The decoy (D) is dominated by the target (T) because it is less attractive than the target along dimension 2 and is not more attractive along dimension 1. According to the asymmetric dominance effect, the addition of the decoy increases the attractiveness of the target relative to the competitor

the decoy. The preference of T relative to C, therefore, increases when D is introduced, in contradiction to both the constant-ratio rule and the similarity hypothesis. The asymmetric dominance effect (Huber et al. 1982) is a robust finding in human studies (Huber and Puto 1983; Tversky and Simonson 1993; Shafir et al. 1993; Doyle et al. 1999; Sedikides et al. 1999), and may result from several psychological mechanisms (Wedell 1991).

An even more striking consequence of asymmetric dominance is that the *absolute* preference for the target may increase when the decoy is added. For example, the introduction of an expensive, decoy (D) microwave oven to a set of options already including a similarly sized, but less expensive, target (T) oven and a small, inexpensive competitor (C) oven, increased the market share of the target oven (Simonson and Tversky 1992). This is in violation of regularity, a most fundamental property of rationality theory (Luce 1977), according to which the absolute preference of an option cannot increase when the option set is enlarged. Regularity is often violated in humans when the set of options is enlarged by the addition of an asymmetrically dominated alternative (Huber et al. 1982; Simonson and Tversky 1992; Tversky and Simonson 1993; Doyle et al. 1999).

Finding context-dependent evaluations in animals, which violate properties of rationality theory, has important implications for understanding animal behavior and ecological processes (e.g., Real 1996; Houston 1997). Shafir (1994) showed that context-dependent evaluation processes of animals could be studied by testing transitivity, in a similar way that transitivity had been used to study human decision making (Tversky 1969), and suggested the same for the asymmetric dominance effect (cited in Real 1996). Here, we investigated the choice patterns of honeybees (*Apis mellifera*) and gray jays (*Perisoreus canadensis*) in asymmetric dominance experiments which were conceptually similar to those performed on human subjects. Specifically, we tested whether the relative (violation of the similarity hypothe-

Fig. 2 Front view of the apparatus used in the honeybee experiments, including a top view of the three layers of the flower top. The configuration shown is of flowers 40/2, 50/3, and 100/3, from left to right



sis) and absolute (violation of regularity) preference of the target increased when a dominated decoy was present.

Methods

Honeybees

Honeybees were tested outdoors in screened flight cages in Columbus, Ohio, from June to October 1996. Individual bees made repeated choices between artificial flowers that varied in their handling costs and in the amount of sucrose solution they offered. We tested for context effects by comparing the preferences of the bees when the choice set included only two flowers versus the same two flowers with the addition of a third flower.

A bee entered the foraging cage (1.6×4.4×2.0 m), which shared a common wall with a similarly sized cage in which the hive was located, through a small (10×10 cm) entrance window. Within the foraging cage, a green wooden table held two green wooden platforms, each of which held a testing apparatus that held three flowers. The position of two flowers could be switched by turning them 180° around a central axis (Shafir 1994); switching the position of three flowers within a foraging bout required a slightly more sophisticated design (Fig. 2). Each platform had a clear plexiglass panel with four holes in a row, 5 cm from one another. This panel could be slid 5 cm in either direction along the platform. Only three holes were exposed at any one time; the fourth hole was covered at either end of the platform, depending on the position of the sliding panel. The panel held two flower bases, each able to hold two artificial flowers, which could be rotated around their central axes. A flower could be moved from one end to the other by lifting it, sliding the panel, and inserting it into the hole that was thus exposed on the other end. The position of two adjacent flowers could be switched by rotating their flower base 180° around its central axis.

By descending into a flower, the bee could reach a feeding well at the bottom. Each well was connected by tubing to a dispensing micropipette, so that the bee could be fed a predetermined volume of 20% sucrose-water (mass solute/mass solution). After feeding, the bee flew from the artificial flowers through an exit window at the top of the cage and returned to the hive.

Artificial flowers

Flowers were constructed from clear plexiglass and consisted of a top (4×5 cm) mounted on a 13-mm (inside diameter) tube that was 40, 50, or 100 mm long (Fig. 2). Flower type refers to the flower's tube length and the volume of sucrose solution delivered during

Table 1 The design of the honeybee experiments. Groups V and L differed in the flower type that was added during test 2. The control group repeated the binary choice in the second test, and then performed a trinary choice in the third test, half as in the V group and half as in the L group. The flower types present in each test refer to the flower's tube length and the volume of sucrose solution delivered during each visit

Group	<i>n</i>	Test 1	Test 2	Test 3
V	15	40/2, 50/3	40/2, 50/3, 40/1	40/2, 50/3
L	16	40/2, 50/3	40/2, 50/3, 100/3	40/2, 50/3
Control-V	8	40/2, 50/3	40/2, 50/3	40/2, 50/3, 40/1
Control-L	8	40/2, 50/3	40/2, 50/3	40/3, 50/3, 100/3

each bee visit. For example, flower 40/2 was 40 mm long and delivered 2 µl per visit. A rolled strip of fiberglass screening (1-mm mesh) inserted in each tube provided traction for the bee when she climbed in and out. The flower top consisted of two clear plexiglass panels mounted on either side of a piece of colored cardboard that was yellow (Y), blue (B), or white (W). Four 8×25 mm Y, B, or W stickers formed an "X" around the hole in the center of each card. Four two-color combinations were used to mark flowers: B on Y, Y on B, W on B, and Y on W, where the first letter represents the color of the "X" and the second letter indicates the background color of the cardboard.

Procedure

Each of 47 individually marked bees experienced three tests, and each test consisted of eight bouts. A bout began when a bee entered the foraging cage and ended when the bee left the foraging cage and returned to the hive after having made a series of flower visits. Each visit consisted of the bee landing on a flower, descending down its tube, and, invariably, ingesting virtually all of the sucrose solution in its feeding well. In each bout, a bee made a mean (\pm SD) of 18 \pm 3.8 choices between two (binary test) or three (trinary test) flower types. In the eight bouts of a single test, the bee encountered the same flower types. The color pattern that defined each flower type was assigned at random from the four available combinations, in a balanced design across bees. Before testing, bees had to be trained to forage from the apparatus. The entrance window to the foraging cage was opened, and the first bee that flew in was marked and trained to forage from the artificial flowers (Shafir 1994). This bee was then tested in successive bouts until the third test was completed.

Test 1 consisted of a binary choice between a 40/2 and 50/3 flower for all bees (Table 1). In trinary tests, we tested the effect

of adding a third flower type (decoy) on the preferences between the two preexisting flowers. Thirty-one bees experienced a trinary choice in the second test. For 16 of these bees (group L), the decoy (100/3) was unattractive in the length dimension. In terms of the relationships depicted in Fig. 1, the 50/3 flower was the target (which dominated the 100/3 flower) and the 40/2 flower was the competitor. For the other 15 bees (group V), the decoy (40/1) was unattractive in the volume dimension. For this group, the 40/2 flower was the target (which dominated the 40/1 flower) and the 50/3 flower was the competitor. Sixteen additional bees initially acted as controls for the changing context, and experienced the binary choice again in the second test.

In test 3, the bees in groups L and V experienced a binary choice, as in test 1. This was designed to test for a background context effect, that is, whether the binary choice in the third test is affected by past experience with a third flower in the second test, or is similar to the binary choice in the first test. The bees that were in the control group during the first two tests experienced trinary choice in the third test; for one half of the bees, the third flower was as in the L group and for the other half as in the V group (Table 1).

Prior to each test, a bee experienced one forced-choice bout with the flower types to be used in the subsequent test (Shafir 1994). During this bout, the bee made an equivalent (plus or minus one) number of visits to each flower type. This forced-choice bout ensured that the bee received equal exposure to all the flower types before the free-choice bouts.

During free-choice bouts, the two platforms were 40 cm apart, each holding three flowers. In binary-choice tests, three flowers of each of the two types were arranged so that each platform held two flowers of one type and one flower of the other type. In trinary-choice tests, each platform held one of each of the three flower types. The bee entered the foraging cage and eventually chose one of the six available flowers. Once the bee entered a flower, sucrose-water was delivered, and the other two flowers on the same platform were covered. When the bee exited the flower, that flower was also covered. Since the three flowers on the platform that the bee had just visited were now unavailable, the bee had to fly to the opposite platform, which contained three available flowers. Once the bee had chosen one of the three flowers available on that platform, the other two flowers on that platform were covered, and the three flowers on the first platform were uncovered. When the bee exited the present flower, it was covered, and the bee flew back to the first platform. After every third choice, the position of flowers on one of the platforms was switched (alternating between the platforms) so that the bee would not develop a position preference. This process was repeated until the bee had made a series of choices, filled her crop, and returned to the hive, marking the end of one bout.

Gray jays

We tested free-ranging, semi-tame gray jays in Algonquin Park, Ontario, Canada, in October–November 1997. These nonmigratory birds live in social groups on all-purpose territories (Strickland and Ouellet 1993), where they occasionally breed cooperatively (Waite and Strickland 1997). They rely on stored food throughout the winter and even feed retrieved hoards to nestlings and fledglings. In a series of previous tests, gray jays have been shown to make decisions that tend to maximize hoarding rate (e.g., Waite and Ydenberg 1994, 1996) or minimize costly errors in choice while hoarding (Waite and Field 2000). Here, we describe simultaneous choice tests where the subjects were required to hop into tubes to gain access to food (raisins).

The tubes

Tubes were constructed from 1-cm mesh hardware cloth (welded wire). The 1.2-m-long tubes were semicylindrical (radius 25 cm) and closed at one end. Three such tubes were placed on the ground in a radial array (45° angles), with the open ends of the tubes

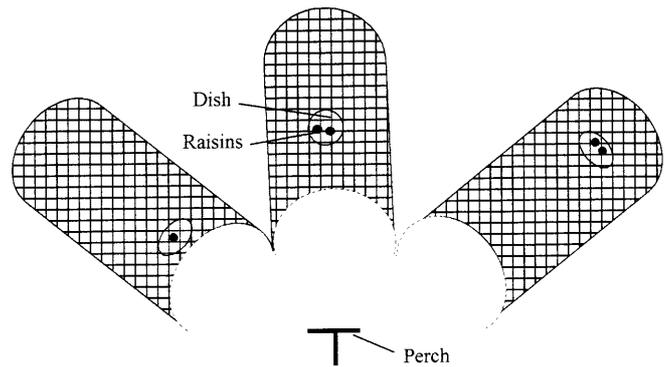


Fig. 3 The apparatus used in the jay experiments (top view). The configuration shown is of tube options 28/1, 56/2, and 84/2, from left to right

Table 2 The design of the jay experiments. Groups trinary-binary-trinary (t-b-t) and binary-trinary-binary (b-t-b) differed in the order of the trinary and the binary tests. The alternatives present during each test refer to the distance along the tube where the plastic disc was placed and the number of raisins that it contained

Group	<i>n</i>	Test 1	Test 2	Test 3
t-b-t	6	28/1, 56/2, 84/2	28/1, 56/2	28/1, 56/2, 84/2
b-t-b	6	28/1, 56/2	28/1, 56/2, 84/2	28/1, 56/2

touching one another and aimed toward a common point (Fig. 3). Subjects could simultaneously inspect the contents of the three tubes by landing on a low (25-cm-high) perch positioned equidistant from the open ends of the three tubes. Food was placed on white plastic discs (radius 8.9 cm), which were positioned at various distances into the tube.

Procedure

Each of 12 uniquely color-banded jays experienced three tests. In each test, the subject made 48 repeated choices either between options A=28/1 and B=56/2 (binary context) or among options 28/1, 56/2, and C=84/2 (trinary context). In the binary context, the subject repeatedly chose between option 28/1 (one raisin 0.28 m into a tube) and option 56/2 (two raisins, 0.56 m), while the third tube contained a disc (0.84 m) but no food. In the trinary context, the third option, 84/2, also contained food (two raisins, 0.84 m). In the terminology used above, option A (28/1) was the competitor, option B (56/2) was the target, and option C (84/2) was the decoy.

Each subject was tested in one of these contexts once and in the other context twice (Table 2). Six subjects were tested in the order binary-trinary-binary and the other six subjects were tested in the order trinary-binary-trinary (144 total choices per subject across the three tests). Following each choice, the jay flew into the surrounding forest, hoarded the raisin(s) in one or more arboreal sites, and then returned to the experimental setup. During the interim, we rearranged the tubes and replenished the raisin(s). Over the course of each 48-visit test, the tubes were rotated eight times through the following left-to-right spatial permutations [where A (28/1), B (56/2), and C (84/2) refer to the three options]: ABC, ACB, CAB, CBA, BCA, BAC. Following the completion of the first and second test with a given subject, we moved the array of tubes approximately 60 m, waited 10 min, and then conducted the next test.

Before testing each subject, we conducted a performance test, where the subject was required to enter one or another of the three simultaneously available tubes during 15 consecutive visits to the experimental setup. During each such visit, all three tubes con-

tained a disc positioned at the same distance and holding a single raisin. The distances were strictly alternated five times through the sequence: 0.28, 0.56, 0.84 m. All jays passed this performance criterion.

Statistical analysis

Analyses were performed using SigmaStat (SPSS 1997). The bee data did not conform to ANOVA requirements and were analyzed using nonparametric tests. Each measure was the proportion choice of a bee in one test (eight bouts). The Wilcoxon's signed-rank test was used to test whether the presence of a third option affected the bees' relative proportion choice for the 40/2 flower (proportion choice of 40/2 divided by the sum of the proportion choices of 40/2 and 50/3). These tests were conducted separately for the 15 subjects in the V group and the 16 subjects in the L group. The Wilcoxon rank sum test was used to compare choice proportions between groups.

For the jays, analyses were performed on transformed (arcsine squareroot) proportions. One-way repeated-measures analysis of variance was used to test whether the presence of option C affected the jays' tendency to choose option B. To perform pairwise comparisons between contexts, we used Tukey's multiple-comparisons test. These tests were conducted separately for the six subjects tested in the order binary-trinary-binary and the six subjects tested in the order trinary-binary-trinary.

Results

Honeybees

Based on previous data (Waddington and Gottlieb 1990; Shafir 1994), we anticipated that bees would show partial preferences between 40/2 and 50/3 flowers. Indeed, bees visited both flower types frequently, and showed stable preferences through time. The proportion of the 40/2 flowers chosen by the control group during tests 1 and 2 were not significantly different (Wilcoxon's signed-rank test, $S=24$, $n=16$, $P=0.23$; Fig. 4a). Since choice proportions were stable for a constant set of options, we could attribute changes in choice proportions when the set of options was altered to the change in the context of choice.

We used the mean proportions over the first two tests (16 bouts) of the control bees as the measure of their choice of the 40/2 flower in the binary phase. The data of the control bees that were later tested as group V in the trinary phase were pooled with the data of group V. The data for the other half of the control bees, which were later tested as group L were pooled with the data for group L.

The proportion of 40/2 flowers chosen in the binary tests that preceded the trinary tests was the same for the L and V groups (Wilcoxon rank sum test, $Z=0.99$, $n_1=23$, $n_2=24$, $P=0.32$; Figs. 4b, 5). When the set of options was expanded (by the addition of a decoy) to three, the decoys took a substantial amount of the visits, and reduced the proportions of the other two options chosen (Fig. 5). However, the reduction in the choice of the other two options was not symmetrical.

For group L, the relative proportion of the 50/3 (T) flower was significantly higher when a 100/3 (D) flower

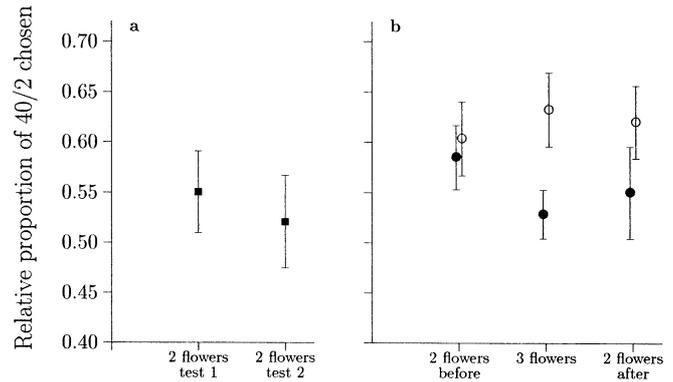


Fig. 4a, b The relative proportion choice of the 40/2 flowers by honeybees (choice of 40/2 divided by the sum of the choices of 40/2 and 50/3) was similar between tests in which the context of choice remained constant, but changed in accordance with the asymmetric dominance effect when the context of choice changed. Vertical lines represent SEs of the means. **a** The preferences of bees in the control group were similar in tests 1 and 2. **b** In the binary test that preceded the trinary tests, preferences were similar for bees in the V group (open circles) and L group (closed circles). In the trinary tests, relative preference for the target, 40/2, of bees in the V group tended to increase with the addition of a decoy, 40/1. Relative preference for the target, 50/3, of bees in the L group increased significantly (and the relative preference for the 40/2 flower decreased) with the addition of a decoy, 100/3. The relative preference for the 40/2 flower differed significantly between the two groups in the three-flower context. In the binary test that followed the trinary tests, preferences were again similar between the two groups.

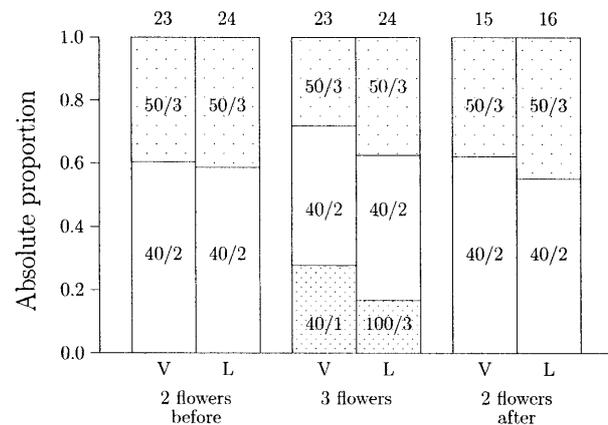


Fig. 5 The absolute proportions of the flowers chosen by honeybees in groups L and V in the binary tests before and after the trinary test, and in the trinary test. Values on top of each column are sample sizes.

was present than during the preceding binary test ($S=77$, $n=24$, $P=0.024$). For group V, the relative proportion of the 40/2 (T) flower tended to be higher, but not significantly so, when a 40/1 (D) flower was present ($S=36.5$, $n=23$, $P=0.28$). The choice of the 40/2 flower relative to the 50/3 flower was significantly greater in the V than in the L group ($Z=2.28$, $n_1=23$, $n_2=24$, $P=0.023$; Fig. 4b). Thus, changing the local choice context by adding a third option affected the preferences between the two preexist-

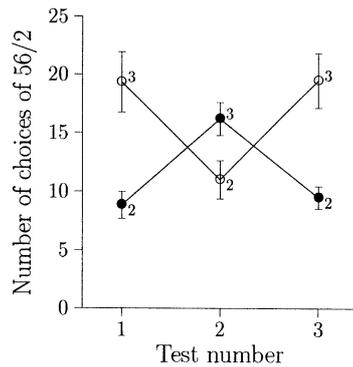


Fig. 6 The number of times that gray jays chose the 56/2 target was greater in a trinary context (3), when the 84/2 decoy was present, than in a binary context (2). Vertical lines represent SEs of the means. Each change in context (from binary to trinary or vice versa) resulted in a significant change in the direction predicted by the asymmetric dominance effect in the number of times that the target was chosen

ing options, in violation of the constant-ratio rule, and the direction of change in preference depended on the characteristics of the added option.

The targets lost relatively less than the competitors from the addition of the decoys, thus violating the similarity hypothesis. Regularity, however, was not violated because the *absolute* share of the targets declined (Fig. 5).

In the binary tests that followed the trinary ones, we tested for an effect of background context (i.e., of the previous experience with the third flower in the trinary test). The proportion choice of the 40/2 flowers approached, although it failed to reach the levels in the binary tests that preceded the trinary ones for both L and V groups, possibly reflecting a weak background effect of the presence of the third flower during the preceding trinary test. The preferences in the latter binary tests, however, were again similar between the two groups ($Z=1.21$, $n_1=15$, $n_2=16$, $P=0.23$; Figs. 4b, 5). Thus, even if some background context effect was evident, it appeared to be weaker than the local context effect observed in the trinary tests.

Gray jays

The gray jays were strongly affected by local context (Fig. 6). The effect of context was significant for the subjects tested in the order binary-trinary-binary ($P<0.001$; normality test: $P=0.52$; equality-of-variance test: $P=0.96$) and for those tested in the order trinary-binary-trinary ($P=0.011$; normality test: $P=0.21$; equality-of-variance test: $P=0.21$). Specifically, the tendency for binary-trinary-binary subjects to choose the target (B=56/2) was significantly stronger in the trinary test than in either binary test ($q_s=7.09$, 6.33; both $P_s<0.015$), and their tendency to choose the target was similar during the first and second binary tests ($q=0.76$, $P=0.86$). Similarly, the tendency for trinary-binary-trinary subjects to choose the target was significantly stronger in the two

trinary tests than in the binary test ($q_s=4.72$, 4.63; both $P_s<0.05$), and their tendency to choose the target was similar during the first and second trinary tests ($q=0.09$, $P=0.99$). Thus, the jays showed a stronger preference for the target in the trinary context than in the binary context regardless of the order in which the tests were conducted. When the decoy (C=84/2) was present (i.e., in the trinary context), it was chosen during only 3.8% of the visits, on average (range: 0–5 of 48 choices), and the absolute number of times the jays chose the target was greater in this context. Thus, the jays violated both the similarity hypothesis and the principle of regularity. There was no evidence of a background context effect, since under similar local contexts (binary or trinary choice), the jays showed similar preferences.

Discussion

We tested the choices of honeybees and gray jays in binary and trinary contexts. According to the theories of rational choice and optimal foraging, the subjective values assigned to two preexisting options should not be affected by the presence or absence of a third option. However, our subjects were affected by the presence of an asymmetrically dominated decoy just like human subjects in analogous experiments (Huber et al. 1982; Huber and Puto 1983; Simonson and Tversky 1992). They showed context-dependent choice and violated the constant-ratio rule. Furthermore, the share of the targets *increased* relative to the share of the competitors due to the addition of decoys that were more similar to the targets than to the competitors, thus violating the similarity hypothesis. The effect was more remarkable for the gray jays, which also violated the property of regularity (i.e., the *absolute* share of the target was higher in the presence of the decoy).

In both the honeybee and the gray jay experiments, the relative preference of the two preexisting alternatives was changed by the addition of the decoy. This contradicts the assumption of proportionality, which underlies the constant-ratio rule, and which has been incorporated into several models of choice behavior (e.g., Luce 1959; see Huber and Puto 1983). According to proportionality, a new item takes its share from the preexisting items in proportion to their original shares (and hence the ratio of their preferences is constant). In our experiments, the relative preference of the target increased with the addition of the decoy. The effect was statistically significant under all experimental conditions with the gray jays and in the L group with the honeybees; in the V group, the effect was in the same direction, but was not statistically significant. Such an attraction effect (Huber and Puto 1983), in which the decoy increases the desirability of items that are more similar to it (like the target), is in violation of the constant-ratio rule and the similarity hypothesis.

If the attraction effect is strong enough, regularity may also be violated, as in the gray jay experiments. In

the honeybee experiments, regularity was not violated, because the *absolute* preference of the target declined in each case. In the honeybee experiments, unlike the jay experiments, the decoys took a substantial share from the options in the original set. Under such conditions, it is difficult to produce violation of regularity (Huber et al. 1982). Apparently, the unattractive third options in the honeybee experiments were not as unattractive to the bees as the third option in the jay experiments was unattractive to the jays. Artificial flowers longer than the 100/3 flower for the L group, or that provide less nectar than the 40/1 flower for the V group, may reduce the choice of these options, and increase the probability of violating regularity. This possibility could be evaluated in future experiments.

In our experiments, we did not observe significant background context effects; there was no influence of past experience on choice. However, in an experiment designed specifically to determine whether choice behavior in gray jays is influenced by background context, a significant effect was found (Waite 2001b). Richter and Waddington (1993) found that background context influenced the dancing behavior of honeybees.

Our findings support a “comparative” method of evaluating options. According to this method, options are not evaluated separately and assigned fixed utilities, but rather the relative value of an option depends on the options with which it is compared (Tversky 1969; Shafir et al. 1989; Richter and Waddington 1993; Shafir 1994). Context-dependent preferences may prove to be quite common, and could conceivably have pronounced ecological consequences. For example, the distribution and abundance of flowering plants is affected by the behavior of their pollinators (Herrera 2000). The introduction and extinction of plant species can alter the competition for pollinators and affect the relationships between the other species in the community. Like the similarity hypothesis, which prevails in economics (Tversky 1972; Huber et al. 1982), niche theory would predict that the species that should lose more pollinator visits from the introduction of a new species are those that are most similar to it. Our results, however, contradict the similarity hypothesis and predict the opposite. Consider, for example, a plant community in which an endangered plant (the target) is suffering from low reproductive success because it is outcompeted for pollinator visits by another plant species (the competitor). Introducing a plant (a decoy) that is more similar to the target than to the competitor, and that is dominated by the target, may actually increase the target plant’s attractiveness to pollinators and hence its reproductive success.

The reproductive success of a plant may also be enhanced by the presence of other plants of the same or different species due to other mechanisms of facilitation (Rathcke 1983). For example, a plant located in an area that is dense with other plants may enjoy higher reproductive success due to increased visitation rates from pollinators that are attracted by the high density of plants (Roll et al. 1997; Bosch and Waser 2001). Similarly, a plant that

is unattractive to pollinators may benefit from the presence of a “magnet” species that attracts pollinators to the area (Thomson 1978; Laverly 1992). The manner in which enlargement of the set of options affects animal choice depends on specific characteristics of the available options and on the animals’ decision-making processes.

Similarities in cognitive processes across taxa (Gallistel 1990; Shettleworth 1998) include those that generate apparent “paradoxes” in rational choice behavior (Shafir 1994; Real 1996; Hurly and Oseen 1999; Waite 2001a). New evidence for violations of rational choice in animals is making an important contribution to the ongoing rationality debate in psychology and economics (Ayton 2000; Stanovich and West 2000). In particular, these findings question the necessity for explanations of such choice phenomena in humans that are based on reasoning or on justifying one’s preferences (Simonson 1989; Wedell 1991; Shafir et al. 1993). Bees and birds are making similar choices, but do not seek reasons or justification for the choices they make. Rather, models that incorporate psychophysical mechanisms may prove more appropriate, at least in explaining animal decision making (Wedell 1991; Bateson and Kacelnik 1998; Shafir et al. 1999; Shafir 2000).

Context-dependent choice may result from a particular cognitive architecture (Real 1991) that is perhaps adaptive in some situations (Wernerfelt 1995; Houston 1997), but the tendency to adjust choice behavior to the presence or absence of irrelevant alternatives has no apparent adaptive value. The phenomenon may be an intrinsic constraint of fundamental decision-making processes (Dukas 1998), and studying such phenomena may shed light on central nervous system functioning. Moreover, behavioral ecology could profit from a better understanding of how context affects the manner in which animals evaluate resources, and from incorporating context-dependent phenomena into models of choice behavior.

Acknowledgements We thank Eldar Shafir for very helpful discussions and comments, and Itamar Simonson and anonymous referees for valuable suggestions. S.S. was supported by an Ohio State University postdoctoral fellowship. The experiments comply with the current laws of the countries in which they were performed.

References

- Ayton P (2000) Do the birds and the bees need cognitive reform? *Behav Brain Sci* 23:666–667
- Bateson M, Kacelnik A (1998) Risk-sensitive foraging: decision making in variable environments. In: Dukas R (ed) *Cognitive ecology*. University of Chicago Press, Chicago, pp 297–341
- Bosch M, Waser NM (2001) Experimental manipulation of plant density and its effect on pollination and reproduction of two confamilial montane herbs. *Oecologia* 126:76–83
- Doyle JR, O’Connor DJ, Reynolds GM, Bottomley PA (1999) The robustness of the asymmetrically dominated effect: buying frames, phantom alternatives, and in-store purchases. *Psych Marketing* 16:225–243
- Dukas R (1998) Constraints on information processing and their effects on behavior. In: Dukas R (ed) *Cognitive ecology*. University of Chicago Press, Chicago, pp 89–127

- Gallistel CR (1990) The organization of learning. MIT Press, Cambridge, Mass
- Herrera CM (2000) Flower-to-seedling consequences of different pollination regimes in an insect-pollinated shrub. *Ecology* 81:15–29
- Houston AI (1997) Natural selection and context-dependent values. *Proc R Soc Lond B* 264:1539–1541
- Huber J, Puto C (1983) Market boundaries and product choice: illustrating attraction and substitution effects. *J Conserv Res* 10:31–44
- Huber J, Payne JW, Puto C (1982) Adding asymmetrically dominated alternatives: violations of regularity and the similarity hypothesis. *J Conserv Res* 9:90–98
- Hurly TA, Oseen MD (1999) Context-dependent risk-sensitive foraging preferences in wild rufous hummingbirds. *Anim Behav* 58:59–66
- Laverty TM (1992) Plant interactions for pollinator visits: a test of the magnet species effect. *Oecologia* 89:502–508
- Luce RD (1959) Individual choice behavior. Wiley, New York
- Luce RD (1977) The choice axiom after twenty years. *J Math Psychol* 15:215–233
- Navarick DJ, Fantino E (1972) Transitivity as a property of choice. *J Exp Anal Behav* 18:389–401
- Payne JW, Bettman JR, Johnson EJ (1992) Behavioral decision research: a constructive processing perspective. *Annu Rev Psychol* 43:87–131
- Payne JW, Bettman JR, Schkade DA (1999) Measuring constructed preferences: towards a building code. *J Risk Uncert* 19:243–270
- Rathcke BJ (1983) Competition and facilitation among plants for pollinators. In: Real L (ed) *Pollination biology*. Academic Press, New York, pp 305–329
- Real LA (1991) Animal choice behavior and the evolution of cognitive architecture. *Science* 253:980–986
- Real LA (1996) Paradox, performance, and the architecture of decision-making in animals. *Am Zool* 36:518–529
- Richter MR, Waddington KD (1993) Past foraging experience influences honey bee dance behaviour. *Anim Behav* 46:123–128
- Roll J, Mitchell RJ, Cabin RJ, Marshall DI (1997) Reproductive success increases with local density of conspecifics in a desert mustard (*Lesquerella fendleri*). *Conserv Biol* 11:738–746
- Sedikides C, Ariely D, Olsen N (1999) Contextual and procedural determinants of partner selection: of asymmetric dominance and prominence. *Soc Cogn* 17:118–139
- Shafir E (1993) Intuitions about rationality and cognition. In: Manktelow KI, Over DE (eds) *Rationality: psychological and philosophical perspectives*. Routledge, New York, pp 260–283
- Shafir EB, Osherson DN, Smith EE (1989) An advantage model of choice. *J Behav Decision Making* 2:1–23
- Shafir E, Simonson I, Tversky A (1993) Reason-based choice. *Cognition* 49:11–36
- Shafir S (1994) Intransitivity of preferences in honey bees: support for ‘comparative’ evaluation of foraging options. *Anim Behav* 48:55–67
- Shafir S (2000) Risk-sensitive foraging: the effect of relative variability. *Oikos* 88:663–669
- Shafir S, Wiegmann DD, Smith BH, Real LA (1999) Risk-sensitive foraging: choice behaviour of honeybees in response to variability in volume of reward. *Anim Behav* 57:1055–1061
- Shettleworth SJ (1998) *Cognition, evolution, and behavior*. Oxford University Press, New York
- Simonson I (1989) Choice based on reasons: the case of attraction and compromise effects. *J Conserv Res* 16:158–174
- Simonson I, Tversky A (1992) Choice in context: tradeoff contrast and extremeness aversion. *J Market Res* 29:281–295
- SPSS (1997) *SigmaStat, version 2.0*, SPSS, Chicago
- Stanovich KE, West RF (2000) Individual differences in reasoning: implications for the rationality debate? *Behav Brain Sci* 23:645–726
- Stephens DW, Krebs JR (1986) *Foraging theory*. Princeton University Press, Princeton, NJ
- Strickland D, Ouellet H (1993) Gray jay. In: Poole A, Stettenheim P, Gill F (eds) *The birds of North America*. Academy of Natural Sciences, Philadelphia, and American Ornithologists’ Union, Washington, DC
- Thomson JD (1978) Effect of stand composition on insect visitation in two-species mixtures of *Hieracium*. *Am Midl Nat* 100:431–440
- Tversky A (1969) Intransitivity of preferences. *Psychol Rev* 76:31–48
- Tversky A (1972) Elimination by aspects: a theory of choice. *Psychol Rev* 79:281–299
- Tversky A, Simonson I (1993) Context-dependent preferences. *Manage Sci* 39:1179–1189
- Waddington KD, Gottlieb N (1990) Actual vs. perceived profitability: a study of floral choice of honey bees. *J Insect Behav* 3:429–441
- Waite TA (2001a) Intransitive preferences in hoarding gray jays (*Perisoreus canadensis*). *Behav Ecol Sociobiol* 50:116–121
- Waite TA (2001b) Background context and decision making in hoarding gray jays. *Behav Ecol* 12:318–324
- Waite TA, Field KL (2000) Erroneous choice and foregone gains in hoarding gray jays. *Anim Cogn* 3:127–134
- Waite TA, Strickland RD (1997) Cooperative breeding in gray jays: philopatric offspring provision juvenile siblings. *Condor* 99:523–525
- Waite TA, Ydenberg RC (1994) What currency do scatter-hoarding gray jays maximize? *Behav Ecol Sociobiol* 34:43–49
- Waite TA, Ydenberg RC (1996) Foraging currencies and the load-size decision of scatter-hoarding gray jays. *Anim Behav* 51:903–916
- Wedell DH (1991) Distinguishing among models of contextually induced preference reversals. *J Exp Psychol* 17:767–778
- Wernerfelt B (1995) A rational reconstruction of the compromise effect: using market data to infer utilities. *J Conserv Res* 21:627–633
- Wiegmann DD, Wiegmann DA, MacNeal J, Gafford J (2000) Transposition of flower height by bumble bee foragers (*Bombus impatiens*). *Anim Cogn* 3:85–89