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## Rational Choice Behavior: Definitions and Evidence

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### Introduction: The Problem of Choice

As humans, we are constantly faced with choices between alternative options. We have to decide which products to buy in the supermarket, what sort of house we want to live in, and even who we would like to meet again following a speed-dating event. These choices are made difficult not only by the sheer number of different options we are faced with, but also by the fact that the options differ in multiple attributes that may affect our decisions. Buying something as seemingly simple as a box of eggs recently, I realized that I had to make a choice based on price, box size, egg size, egg color, freshness, whether the hens were free-range or kept in battery cages, and whether they were fed a conventional or organic diet! Although this kind of problem might at first seem unique to humans living in the modern world, many non-human animals are also faced with complex choices about what to eat, where to live, and who to mate with. For example, a foraging rufous hummingbird (*Selasphorus rufous*) must choose between flowers of different species differing in corolla length and the sweetness and volume of nectar contained; a colony of rock ants (*Temnothorax albipennis*) moving house must choose between potential nests differing in the size of the entrance hole and the darkness of the interior; and a female mouse (*Mus musculus*) looking for a mate has to choose between males differing in genetic relatedness and genetic quality. Studying the choices made by animals in such situations is a major area of research in animal behavior. Researchers want to understand both the proximate mechanisms of choice and the ultimate evolutionary explanations for the choices animals make. The study of proximate mechanisms is predominantly the domain of ethologists and comparative psychologists, whereas the study of the adaptive significance of the choices animals make is the domain of behavioral ecologists.

Rationality is a property of choice behavior that, as we will see shortly, has been used to describe both the mechanisms of choice and the outcome of the choice process. The ancient Greek philosopher, Aristotle, saw rationality as a property unique to human decision making, setting us apart from other animals. However, modern-day biologists and psychologists have extended the concept of rationality to animal choice, and are actively pursuing research into whether animals can be considered rational. In this article, I review the study of rationality in animals and examine what the evidence says about whether animals are indeed rational. However, before we address these questions, we first need to understand exactly what it means to describe a choice as rational.

### What Is Rationality?

It is difficult to provide a concise definition of rationality, because it has been used to refer to different properties of choice in different academic disciplines. Biologists, economists, philosophers, and psychologists all use the term 'rationality' to describe choice behavior, but they define rationality in many different ways. Any student new to the area will be horrified at the bewildering typologies produced by researchers in different fields, and this artilce cannot review the many subtly different definitions of rationality. Instead, I suggest that we can map many, if not most, of the existing definitions of rationality onto two broad categories: first, descriptions of the process of choice, and second, descriptions of the outcome of choice, that is, which option is actually chosen. Thus, in analyzing our hummingbird's choice of flowers, we can focus on either the mechanisms it uses to choose one flower from a set of three, or alternatively on which flower it actually chooses. We can ask whether both the process of choosing and the outcome of the bird's choice can be described as rational. Thus, the two uses of rationality map neatly onto two of Tinbergen's four questions: those of proximate mechanism and ultimate function.

### Rationality of Choice Processes

If you look up the adjective 'rational' in a standard English dictionary, you will find definitions such as: 'Using reason

or logic in thinking out a problem' or 'Endowed with the capacity to reason.' Both these definitions refer to reasoning, which in turn is defined as the ability to think, or to draw conclusions from known facts. These layman's definitions of rationality correspond quite closely with the way philosophers and cognitive psychologists use the term. Interestingly, they are also similar to the definition adopted by Charles Darwin who wrote in his notes, "Rational actions . . . are actions which are required to meet circumstances of comparatively rare occurrence in the life-history of the species, and which therefore can only be performed by an intentional effort of adaptation . . . rational actions . . . serve to meet novel exigencies which may never before have occurred even in the life-history of the individual." Darwin went on to argue that rational action, "Implies the conscious knowledge of the relation between means employed and ends attained" (Darwin cited in Romanes (1882)). In defining rational actions, Darwin contrasts them with what he refers to as 'reflexes' and 'instinctive actions.'

Thus, in describing the process of choice as rational, Darwin and others are implying the use of cognitive mechanisms that we might describe as 'clever' or 'intelligent.' By this, we mean mechanisms that represent information about the state of the world and the goals of the animal, and use this information in a flexible way to solve novel problems effectively. Darwin's definition also implies that conscious intention has to be present for rationality. However, most modern biologists are not happy with the notion of ascribing conscious intentions a causal role in the generation of behavior. Consciousness is a private experience, and consequently we can never objectively observe or measure it in animals. Therefore, most modern research in animal cognition distinguishes between the study of information processing in animals and the study of consciousness. We can ask how animals acquire, represent, and use information in the generation of behavior without asking whether or not this happens via some conscious process. Thus, for the purposes of this study, we will define a *choice process* as rational if the resulting behavior displays evidence of flexible, goal-directed information processing based on representations of the state of the world.

## Rationality of Choice Outcomes

The second use of the term 'rationality' focuses on the alternatives an animal actually chooses, as opposed to the processes responsible for choice. This use of rationality therefore refers to directly observable behavior rather than unobservable cognitive processes. An individual's behavior is defined as rational if it is compatible with the individual maximizing a currency of some type, resulting in internally consistent decisions. This definition of rationality has its roots in microeconomic theory and

has only relatively recently been explicitly considered in the context of animal behavior. I will therefore start by describing what rationality means in economics before exploring how we can apply the concept in biology.

### Economic rationality

The theory of individual decision making developed in microeconomics starts by considering the problem of choosing from among a set of mutually exclusive alternatives (similar to the egg-choice problem with which I opened this study). Economic models of choice assume that when making such choices human consumers maximize a quantity called 'utility.' One can think of utility as a measure of the relative satisfaction an individual derives from a specific resource. However, it is important to realize that utility cannot be measured independent of what people actually choose. Rational choice is simply defined as choice behavior that is compatible with the maximization of utility. If an individual maximizes utility, or indeed any other currency, their choice behavior will be internally consistent in various ways that are considered to be hallmarks of rational choice. These hallmarks include the properties of transitivity, independence from irrelevant alternatives, and regularity. I will briefly describe each of these properties in the following paragraphs.

Transitivity is a property that applies specifically to binary choices. Preferences are transitive between the three options A, B, and C if A is preferred to B, B is preferred to C, and A is preferred to C. For example, if binary choices reveal that I prefer a cherry to a pear, and a pear to an apple, then if my choices are transitive I should prefer a cherry to an apple (see **Figure 1(a)** for an example). If I showed the opposite preference and preferred the apple to the cherry, this would constitute a violation of transitivity (see **Figure 1(b) and 1(c)**).

Independence from irrelevant alternatives is a property that applies when a choice set is expanded. It implies that the preference between two options should be independent of the presence of additional inferior alternatives. For example, if A is preferred to B in the binary choice of A versus B, then the introduction of option C should not affect the preference for A over B (see **Figure 2(a)** for an example). If the relative preference for A over B is altered by the addition of C, this is referred to as a 'violation of the constant ratio rule' (**Figure 2(b)**). If the absolute preference for either A or B increases when C is added to the choice set, this is referred to as a 'violation of regularity' (**Figure 2(c)**).

Thus, we can summarize the economists' definition of rationality as follows. In economics, rationality describes the internal consistency in an individual's choices that results if they are maximizing a currency known as 'utility.' Economists consider transitivity and regularity to be fundamental features of rational choice. Given that one cannot measure utility directly, assessing transitivity and regularity
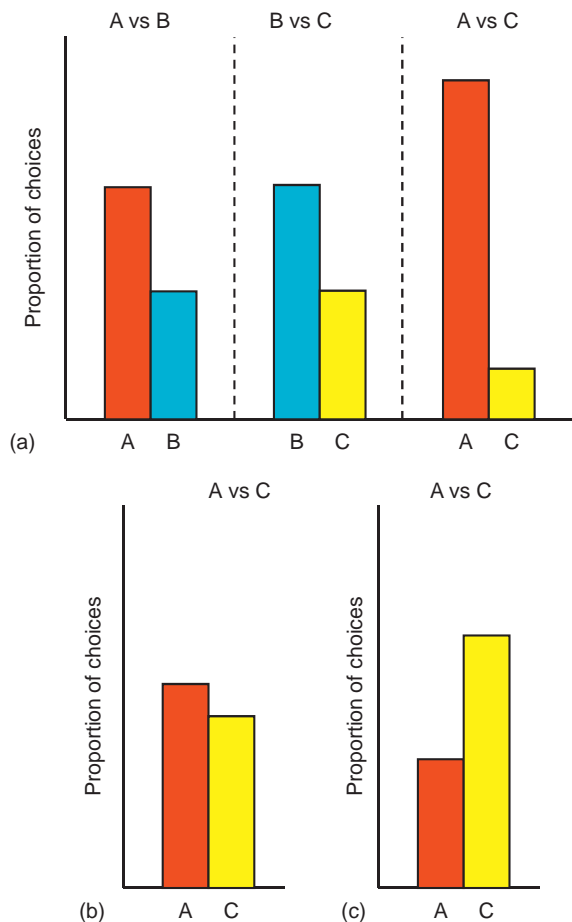
Figure 1   (a) An example of transitive choice: A is preferred to B, B to C, and A to C; (b) an example of a violation of strong stochastic transitivity: the preference for A over C is less than the preference for A over B or B over C; (c) an example of a violation of weak stochastic transitivity: C is preferred to A.
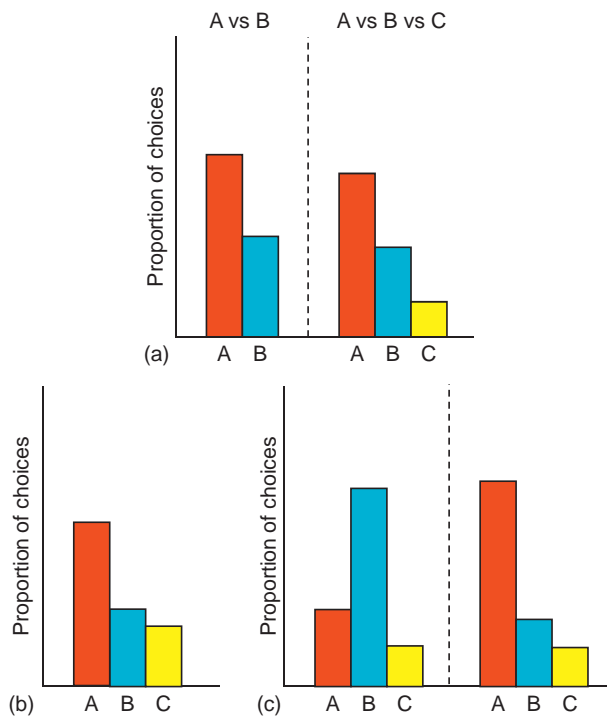


Figure 2   (a) An example of independence from irrelevant alternatives. When the inferior option, C, is added to the binary choice of A and B, the relative preference for A over B remains unchanged; (b) an example of a violation of independence from irrelevant alternatives: the addition of C leaves the proportion of choices for A unchanged but reduces the proportion of choices for B, leading to a violation of the constant ratio rule; (c) two examples of violations of regularity: the addition of option C either increases the proportion of choices for B (first panel) or A (second panel).

will often be the only way to test whether human consumers maximize utility.

### Biological rationality and optimal foraging theory

Given the strong superficial similarity between the kinds of choices faced by humans and animals, it is perhaps not surprising that research on animal choice has drawn heavily on the theories developed to model the behavior of human consumers in microeconomics. However, a major difference between biological and economic models of choice is that they assume different currencies of maximization. In animal behavior, we start with the basic assumption that an animal's behavioral repertoire is ultimately the product of evolution by natural selection. Natural selection favors genetic variants with the highest inclusive fitness; thus, the behavior of an animal observed in the context in which it has evolved should ultimately maximize its inclusive fitness. By analogy with the economists' definition earlier, we can think of an individual that behaves in a way that maximizes its inclusive fitness as biologically rational. Since we assume

that all animals should be ultimately biologically rational, this is in some sense a trivial definition. Ultimately, however this does not matter, because behavioral ecologists take biological rationality as their starting point for more detailed analyses of behavior; the basic assumption of ultimate biological rationality is not under test.

Unlike utility, biologists can, in principle, measure inclusive fitness. However, inclusive fitness is unlikely to be an appropriate currency for computing the costs and benefits of alternative decisions in many circumstances. For example, assume that we want to understand the moment-to-moment flower choices of a foraging hummingbird. The inclusive fitness consequences of the bird choosing a specific flower type are hard for us to measure, because in order to estimate these it would be necessary to record the lifetime reproductive success of birds that fed on this flower type compared with birds that fed on another flower type. Similarly, the hummingbird cannot use its inclusive fitness as the currency it is maximizing when it is making foraging decisions, because the consequences of its choices are not immediately translated into detectable changes in

fitness. We therefore assume that foraging animals must use currencies for decision making that are accessible to them over the time scale of a single foraging bout. The assumption is that natural selection will have favored animals that use currencies for decision making that correlate well with inclusive fitness over the life of the animal.

One of the most common currencies assumed in optimal foraging models is net rate of energy intake. Maximization of this currency is likely to lead to maximization of fitness because both time and energy have clear relationships with fitness: the more energy taken in the more can be used for growth and reproduction, and the less time spent foraging the more is available for other fitness enhancing activities. However, different currencies will be appropriate for different behavioral decisions. For example, in the case of a small bird in winter choosing between safe and risky foraging options, the best currency might be the probability of surviving the night, whereas for a worker bee choosing how much nectar to carry, it might be the ratio of energy gained to energy spent (known as 'efficiency'). The specific currency that best predicts inclusive fitness in a given instance will depend on a number of factors including the biology of the species concerned and the exact behavioral decision being modeled. Research in optimal foraging commonly asks which proximate currency best predicts animal decision making. A classical study by Alex Kacelnik investigating foraging decisions in breeding starlings illustrates this approach.

Given the parallels between economic models and optimal foraging models, it is interesting that the economists' definition of rationality was until recently not explicitly mentioned in the foraging literature; indeed, the word does not appear in the index of Stephens and Krebs' (1986) classic text on foraging theory. There are a number of explanations for this omission. The first is that economists and behavioral ecologists ask different questions: economists want to know whether or not we are rational, whereas behavioral ecologists assume that animals are ultimately rational and want to know which of various alternative proximate currencies they are maximizing. The second explanation is that economists and behavioral ecologists analyze different types of behavioral decisions. The hallmarks of rational decision-making analyzed by economists apply to a one-off simultaneous choices between mutually exclusive alternatives. Whereas the classic prey choice and patch leaving problems analyzed in foraging theory consider situations involving sequential, nonmutually exclusive choices, for which measurements of transitivity and regularity are hard to apply. Finally, behavioral ecologists can measure directly the currencies that they make hypotheses about, so they do not have to rely on indirect measures of rationality (such as transitivity and regularity) that characterize the economic approach to choice.

Although animals seldom face simultaneous choices between mutually exclusive outcomes, arguably there are some situations in which they face such choices. For example, a peahen might assess the qualities of the peacocks displaying on the lek before choosing one of them to mate with, and a hummingbird might weigh up the benefits of two clumps of flowers of different species before committing to one of them for its next bout of foraging. In these cases, we can ask whether the animals' choices display the economists' hallmarks of rational decision making. If the proximate mechanisms underlying animal decision making involve the maximization of absolute currencies, such as for example rate of energy intake, then animal choices should be rational in the economists' sense and display the properties of transitivity and regularity.

Thus, we can summarize the biologists' approach to rationality as follows. Biologists assume that behavior is ultimately rational in that it maximizes inclusive fitness. Behavioral ecologists assume that animal decision-making mechanisms maximize proximate currencies which in turn maximize inclusive fitness. If animals make decisions by maximizing proximate currencies, then their choices should also be rational in the economic sense.

## Are Animals Rational?

Having established what biologists mean by rational behavior, in this section we will proceed to identify what kinds of evidence we need to determine whether or not animals are rational. Given the different definitions of process and outcome rationality explained earlier, we will consider each separately.

### Testing Process Rationality in Animals

The definition of process rationality implies mechanisms of choice that we cannot observe directly. Therefore, tests of process rationality must use observable behavior to draw inferences about unobservable mental states and processes. The challenge in testing whether animals can be described as rational is to find behavioral evidence for flexible, goal-directed information processing based on mental representations of the state of the world. This is extremely difficult, because simple rules and associative learning can often explain behavior that superficially appears to be rational. Investigators have used a number of different species and behavioral tasks to address the question of animal rationality including: tool use and tool construction in New Caledonian crows (*Corvus moneduloides*), scatter-hoarding behavior in western scrub jays (*Aphelocoma californica*), metacognition in Rhesus monkeys (*Macaca mulatta*) and pigeons (*Columba livia*), gaze following and mind reading in chimps (*Pan troglodytes*), to name a few systems where recent progress has been made. In this study, I use transitive inference (not to be confused with transitivity of choice) to illustrate the problems

reaching unequivocal conclusions about process rationality in animals.

### Transitive inference

Many animals need to rank things in a stable series. The ranked entities could be group mates (who is dominant to whom) or food items. For example, within a primate troupe, there may be a stable dominance hierarchy of individuals, or within the territory of a hummingbird, some flower species always have more nectar than others. When an animal has knowledge of such a series, 'transitive inference' refers to the ability to deduce the relationship between two items in the series that the animal has not previously compared directly. For example, if a baboon knows that individual A is dominant to individual B, and that individual B is dominant to individual C, then she is capable of transitive inference if she can deduce that A should be dominant to C. Performing transitive inference apparently involves reasoning using prior knowledge about the relationships between entities in the world to form a conclusion about a novel situation. It therefore captures many of the attributes of process rationality identified earlier. As a consequence, attempts to demonstrate transitive inference in animals have had a central place in comparative psychologists' attempts to test animal rationality.

Investigators have tested transitive inference in a wide range of species including squirrel monkeys, rhesus monkeys, chimpanzees, pigeons, pinyon, and scrub jays, and even cichlid fish (*Astatotilapia burtoni*). Most tests begin by training experimental subjects on what is known as an n-term series task. A three-term task would involve three distinct stimuli, A, B, and C (**Figure 3(a)**). The procedure presents successive adjacent pairs of stimuli from the series (i.e., AB and BC for a three-term series, ABC) to the subject. For each pair, choosing one stimulus produces reinforcement (+) while the other stimulus is unreinforced (−). Thus, for the three-term series, the two trained pairs are A+B− and B+C−. The assumption is that this training will create the linear series A > B > C in the animal's mind. The critical test trial presents a nontrained, nonadjacent pair (in the case of the three-term task, this is AC). If the subject is capable of transitive inference, it should choose stimulus A, on the grounds that it can infer from inspecting its mental representation of the series that A > C.

When trained on such a type of task, most animals do indeed prefer A. However, this preference could equally be explained by a very simple associative mechanism, because during training A has always been rewarded and C never. Hence, the animal could simply be picking the stimulus previously associated with reinforcement, as opposed to reasoning based on inspecting a mental representation of the linear order of the stimuli. For this reason, the standard procedure in tests of transitive inference is to
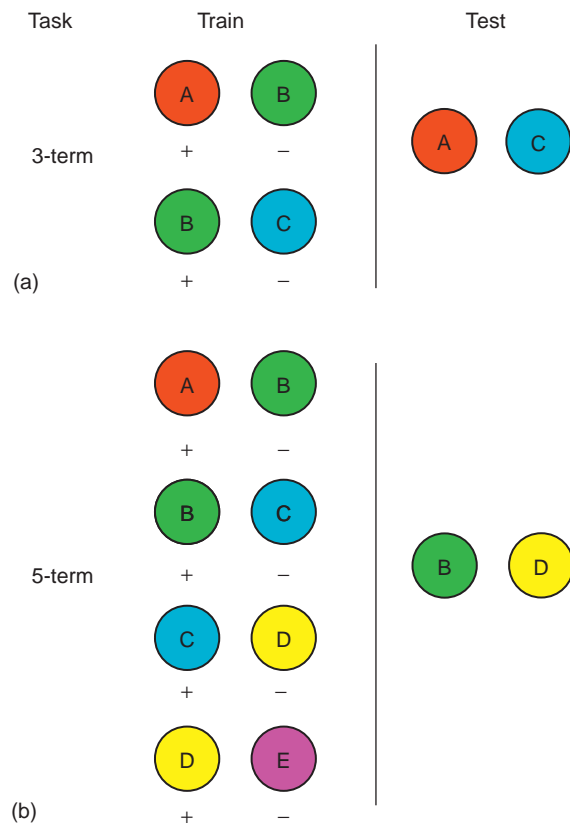


**Figure 3** Reinforcement patterns used in n-term transitive inference tasks: (a) shows a three-term task, and (b) a five-term task.

train the subject on a five-term series (see **Figure 3(b)**). This allows a test trial with the novel pair BD. This test has the advantage over the three-term task that both B and D have been rewarded 50% of the time during training, removing the asymmetry present in the three-term task. When trained on this version of the task most animals prefer B, as predicted if they are capable of transitive inference. Successful performance on this task has been interpreted as evidence for transitive inference in animals.

However, this is not the end of the story. In the course of training, B may have acquired a higher value than D because B is sometimes paired with A, which is always a winner, whereas D is sometimes paired with E, which is always a loser. Thus, if value transfers to B from A and to D from E by virtue of their sometimes being presented together, this could explain why B is preferred to D. It seems that however well-designed the test, it is always possible to come up with an associative account for the animals' behavior that does not require reasoning based on a representation of the series. In studies of comparative cognition, it is usual to apply Lloyd Morgan's Canon which states, "In no case is an animal activity to be interpreted in terms of higher psychological processes, if it can be fairly interpreted in terms of processes which stand

lower in the scale of psychological evolution and development" (Morgan, 1903, p. 59). Following this rule, there is little evidence for process rationality in animals that we could not explain by some simpler mechanism.

## Evidence for Outcome Rationality in Animals

Outcome rationality is simpler to test than process rationality because tests rely on direct observations of what animals choose. As explained earlier, the assumption of biological rationality underpins the whole of behavioral ecology and is generally not directly tested. Instead, behavioral ecologists have focused on testing specific hypotheses about the proximate currencies animals maximize, and this approach has been extremely successful in showing how animal behavior is evolutionarily rational. However, a small number of more recent studies have set out to test whether animals are rational in the economists' sense.

Tests of economic rationality in animals have been inspired by examples of human irrationality. Experiments on human decision making have shown that we tend to make irrational choices when alternative options differ in more than one attribute (as in the egg example with which I started this article). When faced with decisions of this type, a rational decision maker should combine all the attributes into a single currency and choose the alternative that yields the highest value. For example, a hummingbird might choose from a set of flowers that differ in nectar volume, nectar concentration, and handling time. Under an optimal foraging account, we can summarize all these attributes in the single currency of net rate of energy intake. Using this currency, the hummingbird could compare the flowers and make a choice that maximizes net rate of energy intake. However, when humans face complex, multidimensional decisions, they often show violations of transitivity and tend to be influenced by the presence of irrelevant alternatives. For example, an experiment found that purchases of large cans of a high-quality, high-price brand of baked beans increased, and purchases of large cans of a low-quality low price brand decreased, when smaller, relatively more expensive cans of the same high-quality brand are added to the choice set. The small-but-expensive option is an irrelevant alternative, being more expensive and of no better quality than one of the other options, making this result a clear violation of regularity.

One explanation for this irrationality is that rather than combining the attributes into a single currency, we instead resort to simple heuristics for decision making. For example, we might simply choose the option that ranks highest on the greatest number of attributes, ignoring the absolute values of the various attributes. Such heuristics have the benefit of being fast and easy to compute, but they sometimes result in economically irrational choices. Therefore, experiments designed to look for economic rationality in animals have specifically focused on situations in which animals face choices between options that simultaneously differ in multiple attributes of interest.

### Tests for transitivity of choice

Transitivity (not to be confused with transitive inference) is a property of a series of binary choices made between pairs of simultaneously presented mutually exclusive alternatives. Thus, tests of transitivity typically present animals with pairs of choices and study which option the animal prefers. In the first experiment explicitly designed to test economic rationality in animals, Sharoni Shafir presented foraging honeybees (*Apis melifera*) with a series of binary choices between pairs of artificial flowers varying in two attributes both known to affect bees preference: the corolla length and the nectar volume. He found some individual bees that preferred flower A to B, B to C, C to D, but also D to A. Preferring D to A violates what is known as 'weak stochastic transitivity.' Bees that violated weak stochastic transitivity also violated strong stochastic transitivity, meaning that the strength of preference between two flowers adjacent on the scale of utility (e.g., A and B) was larger than that between two more widely separated flowers (e.g., A and C). Similar results have also been found in foraging gray jays (*Perisoreus Canadensis*).

### Tests for independence from irrelevant alternatives and regularity

Independence from irrelevant alternatives and regularity are properties of choice that emerge when we increase the number of alternatives in the choice set. Tests of regularity ask how adding a third alternative to the choice set (a ternary choice) affects preference between two options (a binary choice). My colleagues and I tested the preferences of foraging rufous hummingbirds presented with artificial flowers that offered different volumes and concentrations of nectar. In the binary treatment, birds chose between a high concentration flower (20 μl of 40% sucrose) and a high volume flower (40 μl of 20% sucrose), whereas in two ternary treatments we added a third flower type that was worse than either the high concentration or the high volume flower (10 μl of 30% sucrose and 30 μl of 10% sucrose, respectively) (see **Figure 4(a)**). The additional flowers should be irrelevant to the birds' preference between the high concentration (C) and high volume flowers (V) because they are clearly worse than one of these flowers on both dimensions. However, we found that the third flower type affected both the relative and the absolute preferences for the two options compared in the binary treatment (**Figure 4(b)**). Thus, the birds' preferences violated both independence from irrelevant alternatives and regularity. Interestingly, our results support the idea that the birds use a simple heuristic that ranks concentration and volume dimensions independently,
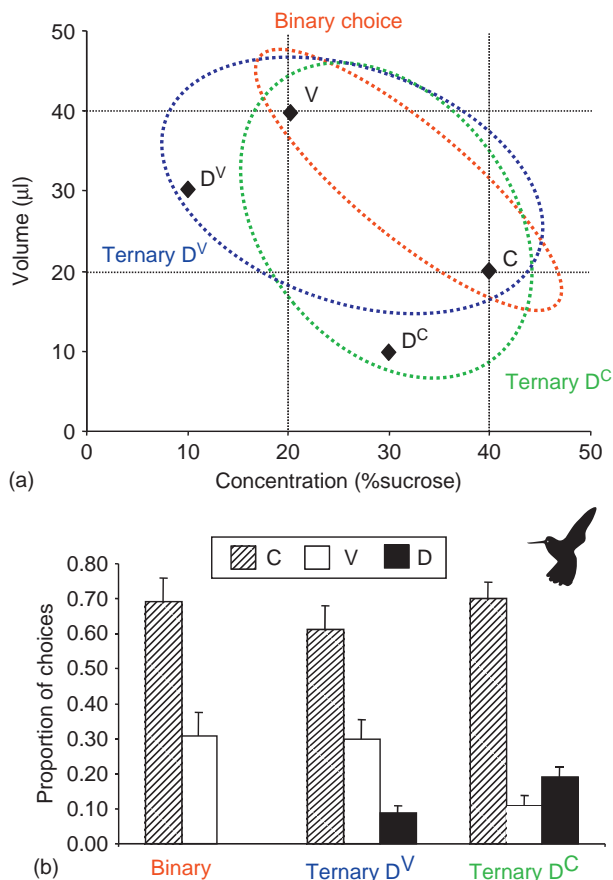
**Figure 4** (a) The four flower types used by Bateson et al. (2003) in their study of hummingbird foraging decisions; (b) results from the experiment: relative preference for V increases in the treatment with $D^V$, whereas relative and absolute preference for C increases in the treatment with $D^C$. Redrawn from Bateson M, Healy SD, and Hurly TA (2003) Context-dependent foraging decisions in rufous hummingbirds. *Proceedings of the Royal Society B* 270: 1271–1276.

because in both ternary choices, preferences shifted toward the flower with the highest relative ranks on both dimensions. Studies using foraging gray jays, honeybees, and starlings, as well as in female green swordtails (*Xiphophorus helleri*) and fiddler crabs (*Uca mjoebergi*) choosing their mates have reported similar results.

## What Does It Mean if Behavior Is Irrational?

The experiments described earlier show that animals are sometimes irrational in the economists' sense. These results imply that animals do not necessarily assign absolute values to alternatives options, but instead the values assigned can depend on the specific set of alternatives available at the time of choice. However, it is important to understand that this in no way threatens our view as behavioral ecologists that animals are ultimately biologically rational. Context dependency could occur for a

number of different reasons. Earlier, I suggested that simple heuristics – such as preferring the option with the highest rank on all dimensions – could explain human and non-human irrationality. Although these heuristics might sometimes lead an animal to prefer a poor alternative (e.g., one that yields a lower rate of energy intake), we assume that natural selection has favored these heuristics because on balance they benefit the animal. Benefits could occur either via increased speed of decision making or a reduced requirement for computational resources in the brain. Other explanations for context dependency have also been suggested. In most studies, for example, the animal makes a sequence of choices, so the options chosen early in the sequence could change the animals state (e.g., reduce its hunger) and thus change the nature of optimal decisions later in the sequence. Thus, it might be possible to accommodate some apparently irrational behavior within a conventional optimal foraging framework.

In summary, although animal behavior can sometimes appear economically irrational, when we consider it in its full ecological context, the biological rationality should become apparent. The value of studying economic irrationality in animal decision making lies in what these studies can tell us about the proximate mechanisms underlying animal choices.

*See also:* Kin Selection and Relatedness; Niko Tinbergen; Optimal Foraging Theory: Introduction.

## Further Reading

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