

Assessment and decision making in animals: a mechanistic model underlying behavioral flexibility can prevent ambiguity

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Understanding how animals make decisions is a fundamental question in behavioral ecology which has cascading effects on how animals respond to environmental variation. An explicit model of the mechanisms of information processing and decision making can help prevent conflated definitions and ambiguous interpretations. Unambiguous definitions are crucial for clear communication between theoreticians and empiricists and for the rapid advancement of studies of decision making. Moreover, employing a clear model of underlying proximal processes will help bridge the gap between cognitive psychology and behavioral ecology and should aid scientific advancement. We present a simple model to guide studies of assessment and decision making. According to the model, individuals assess perceived stimuli and evaluate them for useful information. The association between perceived stimuli and evaluated information involves "assessment rules". Based on evaluated information, individuals can employ trade-offs and make decisions. The association between the result of assessment and observed behavior involves "decision rules". The model clearly emphasizes that the study of decision rules requires knowledge of the results of assessment, and we acknowledge the difficulty of studying assessment. However, without this knowledge, we can only study decision rules when we assume assessment rules between subjects are identical (i.e., with a uniform group of subjects). The simple model can be used to structure the design and interpretation of studies of assessment and decision making and help theoreticians and empiricists work together to understand behavioral flexibility.

1985, Dill 1987, Lima and Dill 1990). To study the decisions and choices animals make, a stimulus (e.g., potential mates, patches, food type or quantity, or predators) is varied, and the resultant behavior observed (e.g., Abrahams and Dill 1989). Often, inferences are then made about processes (usually assessment and decision making) which led to the final observed behavior. Although models of decision making have been suggested for humans (e.g., Das et al. 1979, Hillyard 1984, Montgomery 1989), many behavioral ecologists neglect such models. Consequently, the terms assessment and decision making are frequently conflated.

We define the logical relationships between the terms assessment and decision making and present a simple, yet explicit, information processing model. Theoreticians who model animal behavior (e.g., Stephens and Krebs 1986, Mangel and Clark 1988) must use a range of parameters for perception of risk, food abundance, etc. and often make qualitative assumptions to define this range. In order to facilitate communication between theoreticians and empiricists (Kareiva 1989), empiricists must define their assumptions and clearly present quantitative results. We feel an explicit underlying model will help theoreticians and empiricists communicate and is also required to properly incorporate underlying mechanisms (e.g., Real 1994) into the study of adaptive behavioral responses.

Terminology

In this section we define our use of the terms assessment and decision making, and assessment and decision rules. We compare our use to previous uses of the terms.

Behavioral ecologists view decision making in animals as the process of selecting a behavior while a subject weighs the costs and benefits of alternative behaviors (Dill 1987, Lima and Dill 1990). Animals constantly make decisions: they choose mates (Bateson 1983), select a place to live (Partridge 1978) or forage (Stephens and Krebs 1986), and they decide whether to engage in activities which expose them to risk of predation (Lima and Dill 1990). Results of simple decisions may influence such things as an individual's life span, a species' population biology, and community structure (e.g., Jeffries and Lawton 1984, Kotler 1984, Sih et al.

We use *assessment* to define the process by which animals evaluate perceived stimuli and convert them to what we call informational states. For instance, an animal that encounters a predator evaluates the information acquired during the encounter (including the probability that the predator will attack, the probability that the attack will be successful, etc.) and infers a specific level of risk.

Assessment has also been used to describe the actual behavioral process of acquiring information (Dowds and Elwood 1983, Dick and Elwood 1989, Jackson and Elwood 1989, 1990, Smith and Smith 1989). For instance, Jackson and Elwood (1990) use the term "assessment" when they refer to the manipulation of a shell during inspection, we prefer to call this process "shell manipulation". Assessment can also be used as a noun defining the result of the process of assessment. Green and Marler (1979) call the result of an assessment an "assessment state". To avoid confusion, we refer to the result of an assessment as an "informational state". In the literature on cognition, the result of a previous experience that permits the previous experience to influence future behavior is called a "representation" (e.g., Roitblat 1982, Real 1991). These "representations" are generally viewed as memories (e.g., Roitblat 1982, Cheney and Seyfarth 1990). While we acknowledge that assessments and decisions may be influenced by past experience and/or memories, we focus on assessment and decision making in a short time period to understand how animals immediately quantify the information content of stimuli before making a decision. Thus, we favor the term "informational state" to "representation" for describing the result of an assessment.

Decision making follows the process of assessment and couples an informational state with an observable behavior. When making a decision, an animal evaluates the informational state according to its own current state (e.g., physiological state), and selects a behavioral response. Decision making includes weighing costs and benefits of alternative behaviors and the process often involves trade-offs (e.g., Dill 1987, McFarland 1987, Lima and Dill 1990).

Assessment rules refer to the specific way a given stimulus is associated with an informational state. *Decision rules* refer to the way an informational state is associated with an observable behavior. This definition of decision rules is similar to Green and Marler's (1979) term "transformational rule", in which one set of data is processed to generate a second set. However, Green and Marler focused on communication, and did not distinguish the processes of information acquisition, assessment, and decision making as we do. Assessment and decision rules are "hypotheses" or "models" that the researcher creates about input-output relationships and these can be used to predict animals' responses to varied stimuli (*sensu* Kamil 1994).

The model

We assume three processes are involved in information acquisition and decision making (Fig. 1) and focus on the latter two, because behavioral ecologists tend to be less concerned with the first. First, potential stimuli undergo stimulus filtering to create a set of perceived stimuli. Second, assessment operates on these perceived stimuli to generate "informational states". Third, the decisions (choice of behavior) are based on the informational states, and are made according to some rules. This model is similar to other simple information-processing models (Green and Marler 1979, Hillyard 1984).

1. Information acquisition

Information must be extracted from the environment. Stimulus filtering (Marler 1961) limits the potential stimuli in the environment to a subset of stimuli which can be informative to an individual. For instance, sensory receptors are attuned to respond to certain types of stimuli more strongly than other types of stimuli (Camhi 1984). Other processes (e.g., attentional processes – Crick 1984, Roitblat 1987, Dukas and Real 1993) may reduce the number of potentially informative stimuli to a smaller subset. The study of information acquisition (i.e., the study of the neurobiology and physiology of perception – Ewert 1980, Camhi 1984) and the implications from detection theory (Swets 1961, Green 1970, Williams 1988) are beyond the scope of this paper. We refer only to stimuli that are being perceived (i.e., stimuli that were not eliminated by stimulus filtering). Ontogeny, the individual's physiological state, and sex may all influence the animal directly. For instance, a hungry animal may be weaker and thus more vulnerable to predation. Such factors may also influence sensory processes as well as assessment and decision making.

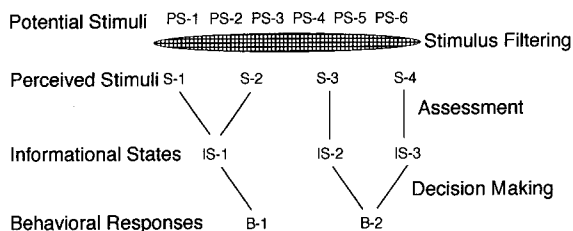


Fig. 1. Schematic representation of the conceptual model which links the perception of stimuli to information assessment, decision making, and the expression of behavior. Terms are defined and discussed in the text. Stages are identified on the left, processes are on the right of the figure. Lines connecting stages reflect the rules used when coupling a stimulus with a behavioral response.

2. Assessment and decision making

We assume that animals have rules for the processes of assessment and decision making (Lima and Dill 1990, Bouskila and Blumstein 1992). Assessment rules, while potentially inaccurate (Bouskila and Blumstein 1992), may be used when acquiring information is costly (e.g., Real 1990). An observable behavior such as avoidance, might be the result of an assessment rule, "if a strong odor of a predator is detected, the risk of predation is high", followed by a decision rule, "if predation risk is high, avoid". The inaccuracy stems from the fact that the predator may not be physically present or able to catch the prey, thus the predator is not necessarily a risk anymore (e.g., Petranka et al. 1987, Kats et al. 1988).

Assessment lends meaning to perceived stimuli and is usually considered important when there is a set of alternative stimuli perceivable by an individual. Examples of factors which may be assessed include: mate quality (e.g., Halliday 1983, Dick and Elwood 1989), patch quality (e.g., Stephens and Krebs 1986), resource holding potential (e.g., Riechert 1982, Dowds and Elwood 1983), and predation risk (e.g., Lima and Dill 1990, Bouskila and Blumstein 1992).

We assume that assessment generates informational states. Degree of risk (for an animal assessing predation risk), attractiveness (for one assessing mate quality), or food quality (for a foraging animal) would be examples of informational states. We assume that these informational states are then used in the decision making process.

Decision rules couple the result of an assessment with a behavior and are subject to trade-offs with other activities and factors. Thus, a decision rule might be, "if the perceived risk of predation is high, stay in a refuge. However, if very hungry, leave the refuge and forage, despite the risk". Since several factors could influence an animal's decision in a given situation, the study of trade-offs provides useful knowledge about factors which may modulate responsiveness to stimuli. Lima and Dill (1990) review a variety of studies related to predation risk which suggest that decision making is influenced by trade-offs.

In general, there are two types of rules: inflexible and flexible (McFarland 1987, Dukas and Real 1993). Inflexible rules do not respond to stimulus variability. An example of an inflexible rule might be a patch leaving rule where the animal leaves after a fixed amount of time (Valone and Brown 1989). We do not address inflexible rules in the model for we view them as the product of natural selection without any current assessment for stimulus variability. In contrast, flexible rules respond to perceived stimulus variability and we focus on flexible rules.

3. Factors which may influence assessment and decision making

Assessment and decision rules may vary: 1) in different species (due to "evolutionary experience"), 2) in different populations of the same species (due to differences in experience or genotype), 3) in different individuals (due to differences in experience, genotype, sex, or age), and 4) within the same individual (due to differences in experience, state, or age). Variation caused by these factors (experience, genotype, age, sex, and state), often prevents unambiguous inferences about assessment and decision making simply by manipulating stimuli and quantifying behavioral responses. Well planned experimental designs (Mead 1988) can control for variation and permit inferences about assessment and decision rules.

Implications for the study of assessment

Traditionally, assessment and decision making have been studied by manipulation. Assessment has been inferred by observing behavior resulting from presentation of different stimuli to individuals (e.g., Davies and Halliday 1978, Leger et al. 1979, Cheney and Seyfarth 1988, Moore and Moore 1988). Attributing the differences observed in behavior to assessment, rather than to decision making, is only possible under certain circumstances.

Because it is likely that factors such as sex, age, state, etc. influence assessment, experimental subjects exposed to different stimuli should be identical, or from uniform groups (same gender, age, rank, etc.) of the same population, or ideally with identical genotypes and individual histories. Parthenogenetic animals may be useful in this respect (see: Crews 1989, Dill et al. 1990). Alternatively, the same animals may be given both stimuli in a repeated measures experimental design (von Ende 1993) and in doing so, control for variation in responses caused by anything other than the stimulus (e.g., Davies and Halliday 1978). In most cases, however, the only option is to compare mixed groups, which are assumed to be an unbiased random mix of the different categories of subjects. In such a case, we assume the groups are virtually identical. If different behaviors are observed as a reaction to different stimuli we can conclude that the stimuli were assessed differently. However, a failure to detect a significant difference in the behavioral responses could be because: a) assessments of the two stimuli were identical, or b) assessments may have been different, but decision rules which weighed costs and benefits of alternative behaviors resulted in the choice of the same behavior (we assume the experiment had sufficient statistical power). As an illustration for option b), one can imagine that predation risk is assessed differently but in spite of the

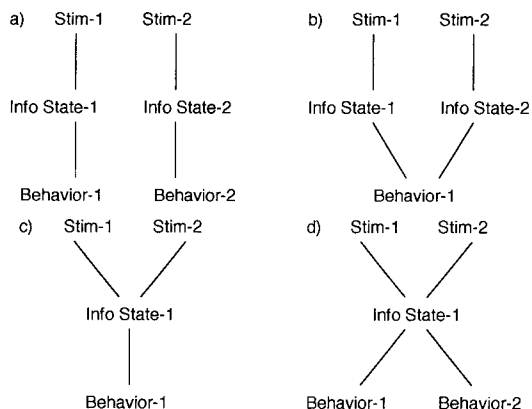


Fig. 2. Schematic path diagrams illustrating the possible outcomes of presenting two stimuli to animals and observing their informational states and resultant behaviors.

difference, a decision rule leads to the same resultant behavior. In many instances there is no way to distinguish between case a) and case b) without quantifying informational states. We conclude that as long as informational states remain unquantified, inferences based solely on observations of different behaviors among uniform or randomly mixed subjects may only be about assessment rules.

Implications on the study of decision making

To study decision making and decision rules, we require knowledge of the result of assessment which we call informational states. Quantifying informational states is generally non-trivial and requires knowledge of the physiology and/or neurobiology of information processing. We discuss possible ways to study informational states after we develop the theoretical basis for the study of decision making. Assuming that we have a physiological or neurobiological measure of informational states (see below), there are four possible outcomes from presenting two stimuli to a uniform group of subjects. We present these outcomes schematically in Fig. 2.

First, there could be different informational states accompanied with different behavioral responses (Fig. 2a). We conclude that the stimuli were assessed differently, and the process of decision making – based on the assessments – led to two different behavioral responses.

Second, subjects exposed to the two stimuli could have different informational states and yet exhibit the same behavior (Fig. 2b). Here, we would infer that the stimuli were assessed differently and that the different informational states led to the same behavior. Trade-offs in the decision making process could have generated this pattern.

Third, subjects may have the same informational state and produce the same behavioral reaction to the two stimuli (Fig. 2c). In this case we would first infer identical assessments of the two stimuli. Second, we would infer decision rules coupled the informational state with the unique resultant behavior.

Finally, subjects could have identical informational states but exhibit different behavioral responses (Fig. 2d). We do not envision this result if subjects were drawn from a uniform group for if they have identical informational states, we expect them to have identical decision rules.

If we were specifically interested in comparing the reactions of two different subgroups (e.g., males and females) to one stimulus, we are obliged to quantify informational states and compare them to the behavioral responses. The potential results of this hypothetical experiment (Fig. 3) are briefly discussed below.

First, the stimulus could generate two informational states and two behaviors in the two groups of experimental animals (Fig. 3a). Here, it would be valid to assume that the assessment rules were different in the two groups, and decision rules coupled an informational state with a resultant behavior.

Second, the stimulus could generate one informational state and two behavioral responses (Fig. 3b). In this instance, we could assume that the assessment rules were identical and each group had a different decision rule which coupled the informational state with a behavior.

Third, the stimulus could generate one informational state and one behavior (Fig. 3c). The inference here is that the stimulus is assessed identically by the two

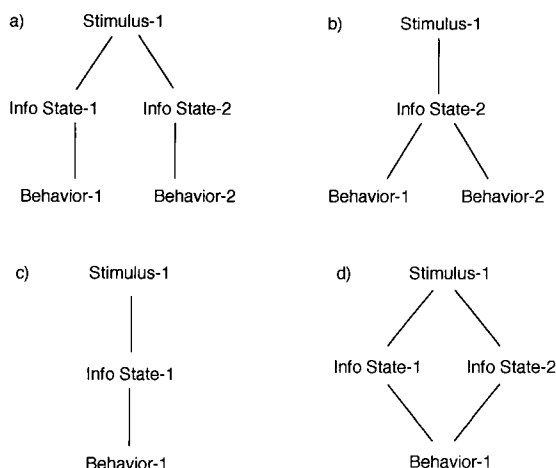


Fig. 3. Schematic path diagrams illustrating the possible outcomes of presenting one stimulus to two groups of animals (e.g., males and females, hungry and satiated, etc.) and observing their informational states and resultant behaviors. For instance, in Fig. 3a, the left path might represent one group's assessment and decision rules while the right path illustrates a second group's assessment and decision rules.

groups and both groups share a decision rule which couples an informational state to a behavior.

Finally, the stimulus could generate a different informational state in each group but produce identical behavioral responses in the two groups (Fig. 3d). Here, we would infer different assessment rules and different decision rules were used by the different groups of subjects.

From Fig. 3 it is obvious that without knowledge of informational states, there is no way we could distinguish between cases 3a and 3b or between case 3c and 3d. Thus, we often require informational states to differentiate the roles of assessment and decision rules.

Conclusions from the model

While we have no desire to succumb to Bolles' (1985) curse on psychologists¹, we must emphasize that experimental design influences appropriate inferences about decision making processes. The model suggests that only the following conclusions can be drawn from specific experimental situations:

1. When several stimuli are presented to a group of organisms (e.g., in a repeated measures design), observing the resultant behavior may permit inferences about assessment only when there are different behavioral responses to the stimuli. No other inferences can be made about decision rules without knowledge of the informational state.

2. With knowledge of informational states, comparisons of the reactions of a uniform group of organisms to two stimuli are possible even if there are invariable overt behavioral responses.

3. With knowledge of informational states, we can compare different groups of subjects reacting to one stimulus. Inferences can be made about their assessment rules and/or about their decision rules.

Quantifying informational states

Several criteria are important to study informational states. Ideally, we would like to be able to measure informational states on unrestrained animals. Our measure should be a continuous measure of stimulus "quality". It should have the potential to vary independently from overt behavioral change. The measure should reflect perceptual processing before a behavioral decision is made. Presently there are no accepted methods

to quantify an animal's informational state. However, current research may ultimately provide techniques which will permit us to quantify informational states.

Autonomic nervous system activity and/or certain event-related brain potentials may meet the above criteria for they reflect the magnitude of perceptual processing in vertebrates. The autonomic nervous system of vertebrates regulates smooth and cardiac muscles and provides glandular control (Brooks 1981, 1983, Carlson 1986). In some vertebrates, activities such as changes in pupil diameter, heart rate changes, hair or feather erection, and galvanic skin responses are under autonomic control. There has been considerable effort in correlating some of these activities with underlying perceptual processes (Brooks 1983). Event-related potentials (ERP) have been implicated as measuring the amount of attention devoted to processing a novel stimulus (Karlin and Martz 1973, Pritchard 1981, Hilliard and Kutas 1983, Wickens et al. 1983, Sommer et al. 1990). Finally, positron emission tomography (PET – Posner and Raichle 1994) may ultimately be useful in quantifying processes and results of assessment, and hopefully, informational states. Much work needs to be done before confidently inferring informational states from these types of measures.

Case studies

We illustrate the utility of the conceptual model as a guide to investigation by re-interpreting previously published studies which have drawn conclusions about assessment rules and/or decision rules. In several cases, our interpretation of a study's findings differed with those made by the authors of the paper. In these cases, the use of our model frequently suggested additional alternative interpretations. Such alternatives could be experimentally studied and eliminated with knowledge of informational states. We classified the studies into three categories:

Category 1: Uniform or randomly-mixed groups were exposed to two or more stimuli leading to different behavioral responses.

Category 2: Uniform or randomly-mixed groups were exposed to two or more stimuli leading to similar behavioral responses.

Category 3: Two or more groups were exposed to one stimulus leading to either different or similar behavioral responses.

Category 1. Davies and Halliday (1978) compared the reactions of male toads (*Bufo bufo*) to high and low pitched croaks. Since each individual was presented with both sounds, identical groups were exposed to each stimulus. The stimuli generated different responses. The authors' conclusions are consistent with an explicit model of assessment and decision making: males assessed the stimuli differently.

¹ "You will never ever discover anything about underlying causal processes, and you will never ever understand the overlying functional significance of anything. You will be forever doomed to be methodologists. You will content yourselves with teaching each other how to do experiments, and you will never know what they mean" (Bolles 1985: 137).

"Category 1" inferences are commonly made. Many other authors inferred assessment in a way that is consistent with the explicit model of assessment and decision making (e.g., Coss 1978, Leger et al. 1979, Kotler 1984, M'Closkey et al. 1987, Pitcher and House 1987, Recer et al. 1987, Cheney and Seyfarth 1988, Jakobsen and Johnsen 1988, Kamil et al. 1988, Moore and Moore 1988, Nishimura 1988, Sugimoto and Tsujimoto 1988, Devries et al. 1989, Marschall et al. 1989, Tome 1989, Valone and Brown 1989, Cuthill and Guilford 1990, Goldthwaite et al. 1990).

Category 2. Wilson (1988) studied bean weevil (*Callosobruchus maculatus*) oviposition behavior. He varied the quality of patches (by manipulating the number of eggs already in the patch) and measured the time for oviposition and the mean number of eggs laid. Wilson found no differences in these behaviors as a function of the initial number of eggs in the patch. The explicit model of assessment and decision making implies two possible interpretations for the observed indifferent behavior. First, the weevils may have assessed the patches accurately, and in spite of a different value assigned to high/low quality patches, weevils were subject to a decision rule or a trade-off that led to the same behavior. Second, the weevils may have acted according to a decision rule without assessing differences in patch quality. By only observing the oviposition behavior of the females, we cannot eliminate either of these alternatives. Quantified informational states would permit additional inferences about the source of the indifferent behavior.

Valone and Brown (1989) studied quitting-harvest rates of desert granivores feeding in artificial patches. They found that some of the species used a fixed time foraging strategy, regardless of the density of food provided. This result could have been caused either by an inability to assess the amounts of food in the patches (Valone and Brown 1989), or by decision rules or trade-offs which coupled distinctive informational states with a single behavior.

Category 3. Abrahams and Dill (1989) looked at the energetic equivalence of predation risk in guppies (*Poecilia reticulata*). They found that the guppy's sex influenced the effect of predation risk on patch choice. One interpretation may be that females assessed risk differently than males; alternatively, females may have assessed it equally, but may have been utilizing different decision rules.

Temeles (1989) studied the response of female northern harriers (*Circus cyaneus*) to conspecific intrusions and found that female harriers who had just fed were less aggressive to floater intruders than hungry females. This could be caused by different assessments of the type of threat posed by the intruders (Temeles 1989). Applying an explicit model of assessment and decision making suggests an alternative interpretation: the threat was assessed similarly, but hunger influenced the decision whether to respond or not.

These studies illustrate that without knowledge of the result of assessment, we cannot separate two alternative mechanistic interpretations. Many other studies we examined generated results with alternative mechanistic interpretations (e.g., Owings and Loughry 1985, Cole 1988, Godin and Sproul 1988, Morgan 1988, Wagner 1989, Cuthill and Guilford 1990, Goldthwaite et al. 1990).

General discussion

Analyzing behavioral processes underlying decision making should ultimately increase our ability to predict responses at higher levels of ecological organization (Real 1994). Future advances in behavioral ecology will likely be the result of the renewed interest in identifying and studying behavioral mechanisms (e.g., Stamps 1991, Real 1994, Wilson et al. 1994, Boissy 1995). The processes by which animals make assessments and decisions are perhaps the key mechanistic questions. Of course there is still considerable utility in determining responses to varied stimuli and treating the decision making processes as a "black box". But, advances in the study of assessment rules and decision rules (the "black box") will likely involve the integration of physiological and cognitive psychological techniques with empirical and theoretical behavioral ecology. Communication between workers in each discipline will be facilitated by a clear model of mechanistic processes. Because this model clarifies the logical relationship between, and identifies the roles of, assessment and decision making, it should help structure future studies of behavioral responses to varied stimuli.

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