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PREVIEW

**EFFECTS OF TWO TYPES OF PRIMING ON VISUAL  
SEARCH IN THE BLUE JAY (*Cyanocitta cristata*)**

by

**Miroslava Belik**

**A DISSERTATION**

**Presented to the Faculty of  
The Graduate College at the University of Nebraska**

**In Partial Fulfillment of Requirements**

**For the Degree of Doctor of Philosophy**

**Major: Biological Sciences**

**Under the Supervision of Professor Alan C. Kamil**

**Lincoln, Nebraska**

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DISSERTATION TITLE

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IN THE BLUE JAY (CYANOCITTA CRISTATA)

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Miroslava Belik

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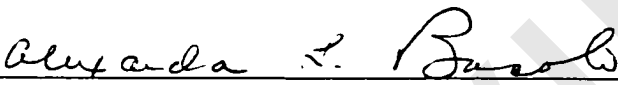
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Dr. Alexandra L. Basolo  
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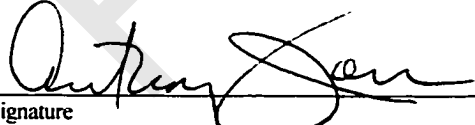
9/27/02

Dr. Alan B. Bond  
Typed Name

  
Signature

9-27-02

Dr. John H. Flowers  
Typed Name

  
Signature

9/27/02

Dr. Anthony Joern  
Typed Name

  
Signature

9/27/02

Dr. Daniel W. Leger  
Typed Name

Nebraska UNIVERSITY OF GRADUATE COLLEGE

# **EFFECTS OF TWO TYPES OF PRIMING ON THE DETECTION OF CRYPTIC STIMULI BY BLUE JAYS (*Cyanocitta cristata*)**

Miroslava Belik, Ph.D.

University of Nebraska, 2002

Advisor: Alan C. Kamil

Foraging efficiency has profound effects on fitness in animals. Increasing components of visual search is especially important for animals that feed on cryptic prey that decrease search efficiency by blending in with the environment. Visually searching predators can use experience during search to facilitate detection of cryptic prey. Two main types of experience have been observed to produce facilitation. One of these is the repeated encounter of a specific type of cryptic prey which is thought to trigger an attentional state that focuses search for a specific prey type. This procedure is also referred to as the searching image or sequential priming. The other type of experience that produces facilitation of cryptic target detection is an association made between the cryptic target and a cue in its surroundings. This environmental cue can also trigger an attentional state which focuses search for a specific prey type. This procedure we refer to as symbolic priming. Priming processes have been studied primarily in humans and little is known about how they function in animals. In human literature, priming has been shown to facilitate the detection of hard-to find targets by providing a cue to the sought for targets' identity. This idea is applicable to animals as well. In the case of sequential priming the cue is the repeated encounter of a specific prey type and

in symbolic priming the cue is the environmental cue associated with a specific prey type.

The experiments described here address both sequential and symbolic priming in blue jays searching for cryptic prey stimuli using a semi-natural operant procedure. Results suggest that the two priming procedures are based on different cognitive mechanisms. Although each procedure results in facilitation of target detection, there is an interaction or interference between the two types of priming when they are used in conjunction. These experiments provide some of the first evidence of how different types of experience affect the detection of cryptic targets in animals.

PREVIEW

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PREVIEW

## **Chapter 1. General Introduction**

Studies of the adaptive value and evolutionary consequences of behavior have been the focus of much of the biological research in animal behavior while the proximate processes that drive behavior have not received as much attention. However, in the last decade there has been an increase in interest in the cognitive processes that underlie behavior both in the field of biology and psychology and the need to synthesize research from the two disciplines has been pointed out by many (Kamil 1983; Real 1993; Shettleworth 2001). Although both biology and psychology seek to answer similar questions, the different histories of these disciplines, including different methodology, terminology and hypothesis testing, make truly integrated experiments rare. “Cognitive ecology” has been proposed (Real 1993) as a term describing a research program synthesizing studies of cognitive mechanisms with ecologically relevant behavior. The experiments included in this dissertation combine research and methodology from both disciplines to study how blue jays search for cryptic prey.

The focus of this research is on procedures used by animals to increase efficiency in detecting hard-to-find items. This chapter will serve as a general introduction to the experiments presented in the following chapters. Because the subjects of the research in this dissertation and of most studies relating to this subject are birds, the most extensive part of this chapter will focus on insectivorous birds searching for food, although examples of these procedures in other animals will also be addressed.

### **Using environmental cues during foraging**

Animals living in a homogeneous environment that is filled with continuously available resources would have no need for mechanisms to facilitate search. However, most animals live in a variable, heterogeneous environment, in which tracking environmental variables to find important resources may be essential to survival (Dusenbery 1992).

In a classic field experiment with great tits during the breeding season, Royama (1970) found that the birds were “conditioned” to specific sites where their preferred prey was most often found. He observed that each successional period of the season was characterized by specific prey types being brought to the nest, most of which inhabited very specific niches of the environment. For example, early in the season the tits focused their hunting mainly on oak foliage, in the middle of the season on blackthorn, hawthorn and ash trees, while at the end of the breeding season they searched primarily on ground vegetation. Learning where to look for the appropriate food resource at the right time of the breeding season is therefore extremely important for the tits.

This ability to track environmental resources may not only be more important to animals at specific time periods, but more generally, may also be more important for some animals than others. For example for animals such as birds, monkeys and humans, environmental complexity has been hypothesized to be an important catalyst in the evolution of cognitive complexity (Shettleworth 1988). In

addition, generalist foragers such as species of Paridae and Corvidae are also thought to exhibit greater abilities than specialists (Robinson and Holmes 1982; Heinrich and Collins 1983). Generalists, for example, may have a greater selective pressure to be able to discriminate cues which signal the location of prey in a continuously changing environment than specialists who restrict their search to specific patches. Emsberg and Wilson (1978) also found that among bats, species that primarily feed on patchily distributed food that is both spatially and temporarily unpredictable tend to have larger brains sizes relative to body size than those that feed on more uniformly distributed food.

The adaptive advantages of learning during foraging have been debated over the years (Johnston 1982; Kamil 1983). Although most agree that learning about relevant cues in the environment confers an important advantage in terms of reproductive success, there is very little available data to support this idea and very few studies have addressed the adaptive value of learning skills directly (Orians 1981; Kamil and Yoerg 1982; Kamil 1983). However, there is evidence from field experiments that points to the importance of learning on survival and mortality rates. These include observations of high mortality of some juvenile birds during the first year of independent foraging, as well as lab experiments which show that inexperienced birds are much more inefficient at handling the prey types which results in significantly higher handling times (Sullivan 1988). Life history characteristics may also be affected by learning, as in some species of predatory birds in which breeding may be longer delayed because a significant degree of skill

in catching prey is required (Ashmole 1963). A few insect studies provide some experimental evidence on the fitness consequences of associative learning. Dukas and Bernays (2000) demonstrated that learning increased the growth rate of grasshoppers compared to a treatment in which learning was not possible which could translate to fitness benefits. In addition, in a different experiment with parasitoid flies, Dukas and Duan (2000) showed that flies that were allowed to learn about appropriate egg laying sites laid a significantly greater number of eggs than those that did not.

The benefit of learning, including the ability to track environmental cues also has costs. In the case of foraging for resources costs may include energetic costs such as making mistakes during acquisition or missing other valuable resources. Although relying on salient cues may be essential, making mistakes such as when responding to wrong cues or the right cues at the wrong time may also be very costly to the animal. Comparative studies relating differences in learning ability to differences in environmental variation among closely related species would be especially valuable to achieve further insights into the evolution of learning during foraging.

Optimization models have been used in many analyses of adaptive behavioral traits in animals and may also provide a powerful tool into the study of how animals learn to use environmental cues during foraging. Kamil (1983) proposed that the synthesis of data from studies traditionally collected by psychologists on learning, with the optimal foraging models developed by

behavioral ecologists, would make a great contribution to our understanding of the foraging behaviors of animals. Models based on the optimal foraging theory assume that the efficiency, or net energy gained relative to the time and energy spent while feeding, is maximized by natural selection (Emlen 1966; MacArthur 1972; Pyke, Pulliam et al. 1977). Foraging decision making should therefore evolve to maximize net energy intake during foraging. These foraging decisions include three main aspects of search: where to forage, what to forage on, and when to leave and search someplace else (Pyke et al. 1977). The classical OFT models include basic assumptions such as: an animal has perfect knowledge of the parameters of the environment, the prey types are instantaneously recognizable, and have a fixed handling time which is independent of the rate of encounter between predator and prey. These basic assumptions have also attracted much of the criticisms of optimality models including that they are too simplistic and unrealistic.

Later models however, relaxed some of these assumptions to provide more realistic models for ecologically meaningful behaviors such as those influenced by experience and learning (Hughes 1979; McNamara and Houston 1985), as well as by encounters with cryptic prey (Erichsen et al. 1980). These models are powerful because the relative contribution of the costs and benefits of each of these factors have to be made explicit and can be used to determine how animals might use these under different conditions. In cases in which the costs seem disproportional to the benefits, an animal may be using some strategy or rule of thumb that may become

more obvious after performing this type economical analysis. For example, modeling an animals' movements as it travels in its environment to find a resource becomes a very difficult and complex task (Dusenbery 1992). How does the animal keep track of all this information? The answer may be found in considering the use of environmental cues which can make search for resources much more efficient as certain features in a non-uniform environment can be associated with a food or prey item. Similarly, unless a cryptic prey item is very abundant or very valuable there is a considerable cost in terms of time, handling and mistakes in search for it. If the cryptic items are valuable or greatly abundant it may pay an animal to pay some of these costs to capture these. Modified optimality models based on signal detection theory are another powerful tool to look at these types of questions. These models have an advantage over optimal foraging models because they allow for more complex and realistic situations by permitting degrees of crypticity for different prey types as well as decision criteria of the predator (Getty et al. 1987). In summary, optimality models could provide an effective way to study the use of environmental cues in an ecological, evolutionary perspective.

### **What is priming and why is it important?**

Priming is a term primarily used in psychological literature and has been studied most extensively in humans. Although priming is not confined to visual tasks, it has been studied most extensively in the visual modality and has been defined as “a pre-trial activation of a targets' features”, in other words a procedure



that facilitates the detection of a specific, hard-to-find target. Functionally, priming can be described as a procedure based on experience that results in the facilitation to detect a cryptic target or prey item. This experience refers to an experience with a cue predictive of the target. This cue can be the repeated encounter of a specific target (as in the searching image procedure) or an encounter of a specific target in a specific context or in association with some abstract cue. This facilitation of target detection is thought to occur as a result of a cognitive process in which attention is focused on the sought for target or its features. The use of priming to locate food items or cryptic targets has been demonstrated in several animal species including humans (Posner and Snyder 1975), bees (Menzel 1990), pigeons (Bond 1983) and blue jays (Pietrewicz and Kamil 1979) and several types of priming may be available to animals.

Priming may therefore be the procedure responsible for the use of environmental cues by animals searching for food or other hard to find resources. Because priming is based on experience and/or learning it also has costs (Posner and Snyder 1975). This is because priming is thought to evoke an attentional mechanism that directs an organism to biologically important features of the environment, which also means that other features of the environment will not be processed (Dukas and Ellner 1993). I will discuss two main types of priming that animals can use, the possible costs and benefits of each, and the specific conditions under which each might be used.

## **Sequential Priming**

Sequential priming refers to the procedure of experiencing a hard-to-find target in a sequence which results in the facilitation of its detection in future encounters. It is also thought to be the procedure that generates the searching image effects observed both in the field and the laboratory. Based on observations in a field study with great tits, Tinbergen (1960) first proposed the idea of the searching image. He noted that the birds brought back to the nest a disproportional number of the most abundant prey types and tended to overlook the rarer types. He hypothesized that the birds were hunting by “searching image” and argued that visually searching birds possess a perceptual mechanism which is activated during frequent encounters with a prey type and allows the birds to learn the key visual features of a camouflaged prey type while also filtering or blocking out other visual stimuli. Following Tinbergen’s field study, many laboratory experiments have substantiated the searching image phenomenon, showing that a repeated encounter with a cryptic target facilitates its detection (Pietrewicz and Kamil 1979; Blough 1989; Blough 1991; Bond and Riley 1991; Blough 1992; Plaisted and Mackintosh 1995; Langley 1996; Langley, Riley et al. 1996; Kono, Reid et al. 1998; Bond and Kamil 1999). The searching image hypothesis garnered much interest in the scientific community because it has far reaching ecological influence including the generation of apostatic selection (Bond and Kamil 1998), and the evolution of prey polymorphism (Bond and Kamil 2002).

Although the searching image has been studied primarily in birds searching for cryptic prey or grains, evidence of this process has been described in other animals, in various circumstances, as well as with different modalities. For example, “trawling” bats may be using an auditory searching image when echolocating for auditorily “cryptic” prey hidden on moving water (Siemers, Stilz et al. 2001). Skunks use olfactory search images to locate small prey item over long distances (Nams 1997) and even Sea Lions develop a searching image for their predator, the killer whale (Baird and Stacey 1989). In addition, insect pollinators may use a searching image to locate flowers, which may be the driving force behind the evolution of flower constancy (Goulson 2000).

Blough (1989) was the first to coin the term “sequential priming” and argued that the searching image effects could be explained on the basis of an attentional priming process in which the target representation is activated during a repeated encounter with the specific target type. This activated representation then facilitated the detection of the target type by increasing discrimination accuracy and reducing reaction time. Plaisted (1997) further argued that an attentional account for sequential priming must also show interference in the ability to detect alternative targets. This is based on the limited capacity model of attention which states that attentional search will facilitate the detection of a target at the expense of some reduction in performance on other targets (Broadbent 1958; Broadbent 1971). Subsequently, Bond and Kamil used a probe trial technique to generate data that

met Plaisted's attentional priming requirement by demonstrating a decrease in performance on alternative targets.

Although there is general agreement that search image effects are generated through priming, the attentional cognitive processes involved are not well understood. For example, it is still unclear whether this process is a learned process based on experience and resulting in expectation, or if it is a stimulus-based low-level perceptual process also termed perceptual sharpening. Langley (1996) showed that pigeons searching for types of grain attend to specific features of the grain such as shape and color. It is possible that the internal representation of that target becomes more detailed and serves as a better cue during repeated encounters. It is therefore possible that the cognitive mechanism behind this process is a direct result of encountering the same "pattern" and could be characterized as a "bottom up" process, or implicit low level learning process based on the visual properties of the stimulus (Shiffrin 1988). Although Blough and Lacourse (1994) did not find data in support of this idea, the target stimuli used in their experimental set-up (alphanumeric characters) may have been too simple to show these effects.

Identifying the costs and benefits of priming is important not only to make predictions about foraging decisions of animals but also to identify the important factors affecting these decisions. For example, the obvious benefit of sequential priming is facilitation during the search for prey, however this facilitation only occurs in specific circumstances such as when prey are cryptic, or under high attentional load. This crypticity requirement has been demonstrated in many

studies (Dawkins 1971; Reid and Shettleworth 1992; Bond and Kamil 1999).

When the prey are easier to detect, the cognitive load decreases and there is no longer a need for the priming (Shettleworth 1988; Kono et al. 1998). This also implies that there is a cost to this type of priming that is balanced only by the benefit under cryptic conditions. Another important cost of attentional priming is the missing of alternative, valuable prey types (Dukas and Kamil 2001). Priming results in a focus of attentional search for a specific prey type which can also interfere with the detection of other valuable prey items. Therefore switching to a new searching image may be costly and may depend on factors such as the relative frequencies, crypticities, and value of prey types.

### **Symbolic Priming**

In symbolic priming, the “pre-trial activation of a targets’ feature” takes place when a “neutral” or abstract cue becomes associated with the sought-for target or resource and facilitates the detection of the target in future encounters. While in sequential priming, the cue and the target are one and the same and the priming takes place through repetition, in symbolic priming an association is formed between two different stimuli during the search for the target. When the target stimulus is reliably found in association with another more salient or discriminable cue, this cue serves as the prime to the target in future searching opportunities.

Symbolic priming is the likely process behind the use of environmental cues to find hard-to-find items during foraging. For example, an encounter with a certain prey type on a specific background or in a specific microhabitat can serve as a cue in future detections of that prey (Rashotte et al. 1987; Kono et al. 1998). Royama's (1970) field observations provide a good example of how birds can learn to associate specific habitat types or tree types with the type of prey that is usually found there. Based on these associations the birds perform searches based on specific habitat types to find the specific prey types that they need at different stages of the breeding period. Heinrich and Collins (1983), using a semi-natural set-up, showed that chickadees are also able to learn to preferentially forage on trees with caterpillar-damaged leaves, especially when the prey types were highly cryptic or hidden. The birds were at least seven times more likely to find a prey item when searching near damaged leaves than when searching in other areas. Real et al. (1984) found that blue jays are extremely good at discriminating insect damage from other types of leaf irregularities, as well as at generalizing from very few examples of insect damage. Interestingly, caterpillar feeding behavior such as leaf-clipping at the petiole, consuming the whole leaf, feeding along the edge, and feeding at night may have evolved as a result of selective pressure from predators that can use irregularities which result from insect damage as a foraging (symbolic) cue.

As with sequential priming, symbolic priming may be a very general process used by many animals besides birds searching for cryptic prey.

Hummingbirds use visual cues when foraging for nectar and distinguishing between plants with nectar and nectar-robbed plants (Irwin 2000). Bees and other pollinator insects use visual cues to find specific flowers high in nectar (Gould 1985) and butterflies use leaf shapes to locate appropriate plants (Papaj 1986). The sensitivity of ungulates to cues that signal food locations has also been used by livestock and land managers to control animal distribution problems by providing animals with visual cues which not only affects distribution of the animals but also increases foraging efficiency (Howery et al. 2000).

Although the process of symbolic priming has been primarily studied in the realm of human perception (Beller 1971), there are a few animal studies that demonstrate how this process operates in search. In operant experiments with pigeons searching for alphanumeric characters among distractors, Blough (1991) demonstrated that pre-trial abstract cues facilitated the detection of alphanumeric targets among distractors. The birds were faster when a reliable cue (a black and white pattern framing the display during the trial) was paired with the target letter than when the cue was unreliable.

As with sequential priming, Blough (1989) proposed an attentional mechanism behind symbolic priming. The pigeons in her experiments were much faster at locating the prey types during trials in which a cue signaled the identity of the target than during ambiguously cued trials. In addition, visual cues also inhibited the detection of alternative targets. Similar to sequential priming, Blough concluded that advance information about a target modifies an attentional

mechanism that facilitates the detection of a target but also carries an inhibitory (interference) cost in processing alternative targets.

A similar type of priming to symbolic priming is spatial priming. Both of these types of priming can also be classified as associative primes. This type of priming is functionally identical to symbolic priming but instead of the association of the sought-for target with an abstract visual cue the association is made with a specific spatial location such as one area of the meadow or a specific segment of a tree. In some ways, these two types of priming are very similar because visual cues can be used to calculate locations. However, there have been few studies looking specifically at this type of priming. Bees for example return to specific locations where they have encountered valuable nectar resources. Croze (1970) and Murton (1971) have anecdotal evidence that crows and pigeons also return to specific locations where they have found food in the past. Great tits have also been observed to frequent particular locations where food is more likely to be found (Royama 1970; Krebs 1972). Although empirical evidence is scarce, Alcock (1973) demonstrated that when location signaled the presence of prey, red-winged blackbirds were found to be highly sensitive to location cues associated with specific prey types (mealworms or seeds), and visited locations associated with their preferred prey type more frequently. In an operant experiment with pigeons, Blough and Lacourse (1994) also observed priming effects of location cuing which facilitated the detection of alphanumeric targets among distractors. Most other studies on location cuing have been performed on human subjects and show strong