FACTORS INFLUENCING THE USE OF SEARCHING IMAGES BY BLUE JAYS HUNTING FOR CRYPTIC PREY

by

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University of Nebraska, 2002

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Insect-eating birds can use searching images to detect cryptic prey. That is, they can learn what the prey looks like, and attend to certain visual features of the prey in order to more easily find additional items of the same type. Much of the research in this area has focused on explaining the mechanisms that facilitate prey recognition. Recently, however, researchers have begun to demonstrate that predators utilizing searching images can favor the evolution of polymorphisms in prey populations. To better understand how predators and prey interact, it is important to understand the variables that influence the effectiveness of searching images. In the following chapters, research investigating several factors is presented. The importance of the degree of resemblance in appearance of two prey types is discussed in Chapter 2. In Chapter 3, the effect of the elapsed time between encounters of the same prey type is discussed. Finally, the effects of prey symmetry are discussed in Chapter 4. Three main conclusions can be drawn from these studies. First, prey types that are very similar in appearance may fall into the same searching image, and they may suffer equal predation rates as a consequence. Second, searching image effects in blue jays can be long-lasting. Third, while crypticity of prey has great influence on searching image effects, effective camouflage may be achieved regardless of pattern symmetry.

The results suggest that prey need to evolve relatively large differences in color pattern to escape a predator's search image. The results also show that blue jays retain searching images for longer durations than pigeons, perhaps as a result of the differences in the distribution of the foods that the two groups of birds search for. Finally, symmetry of prey seems to be less useful for blue jays than predicted, although it remains unclear whether there are large differences in the ways that humans and birds perceive symmetry. In addition, while highly effective background matching seems possible regardless of symmetry, small differences in prey crypsis may have important consequences.

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CHAPTER 1: AN INTRODUCTION

Through multiple encounters with a single cryptic prey type, predators may learn to associate features of that prey type into a mental template. Predators using such a "searching image" can scan the environment in search of additional prey items of that type, leading to greater search efficiency (Tinbergen, 1960). The topic of hunting by searching image has been of interest to ecologists and evolutionary biologists for over four decades (Tinbergen, 1960; Allen & Clarke, 1968; Dawkins, 1971; Pietrewicz & Kamil, 1979; Fullick & Greenwood, 1979; Gendron, 1986; Guilford & Dawkins, 1987; Bond & Riley, 1991; Reid & Shettleworth, 1992; Bond & Kamil, 1999), and the behavior, commonly studied in birds, may be both a cause and an effect of the coevolution of predators and prey. Some prey items are quite cryptic, so predators are under pressure to use their cognitive abilities to maximize detection. For example, they may use selective attention to the visual features of one prey type. Cryptic prey, as a countermeasure, may be under pressure to avoid detection by predators that search for any one prey type. Thus, hunting by search image is viewed as one of several explanations for prey polymorphism.

Despite the level of interest, there are a number of obstacles that have complicated the study of this behavior and related issues. Generally speaking, the problem lies in demonstrating causal relationships. It is quite difficult to demonstrate that the observable adaptations of either birds or their prey are the direct result of their conflicts in previous generations. Similarly, given that there are multiple hypotheses for the maintenance of polymorphism, it is difficult to isolate the role played by predators using searching images.

Many questions about the history of the coevolution of predators and prey are likely to remain unanswered for some time, but real progress is being made in the area of understanding the sort of selective pressure exerted by predators that hunt by searching image (Pietrewicz and Kamil, 1981; Bond, 1983, Cooper & Allen, 1994; Bond & Kamil, 1998). By designing experiments that isolate this process from others, particularly through the use of operant techniques, the cognitive abilities of the predators are becoming clearer. Also becoming more clear are the sorts of factors that influence the effectiveness of such a strategy, such as prey crypticity (Blough, 1989; Bond & Riley, 1991; Reid & Shettleworth, 1992) and background cuing (Kono et al., 1998).

My dissertation attempts to address three questions concerning the relationship between blue jay foraging tactics and the appearance of their prey. The first experiment manipulated the degree of resemblance between two prey types in a polymorphic population to explore effects on searching image use. The second experiment manipulated inter-prey-interval to investigate the duration of searching images. The third experiment addressed factors that are likely to influence whether a predator will adopt a searching image for a given prey type. Specifically, it asked whether symmetrical prey items are more likely to become targets of search than asymmetrical prey items.

Coevolutionary Arms Races:

Over many generations, one may expect that through the process of natural selection, predators should become better able to detect and capture prey. At the same time, it seems reasonable that prey that have traits that enable them to avoid detection and escape when chased are more likely to pass their genes to future generations. Thus it seems that predators and prey should co-evolve with adaptations and counter-adaptations (Dawkins & Krebs, 1979; Slatkin & Maynard Smith, 1979; Endler, 1991).

Unfortunately, it is far more difficult to test hypotheses concerning what happened in the past than it is to generate them. Peter Abrams (1996) has argued that much of our empirical knowledge of predator-prey evolution comes from experiments in population cages involving short generation times. These experiments tend to be focused on parasitoid-host systems, which may differ from the more traditional predator-prey models. Abrams also cautions against the use of the fossil record, which he asserts gives an incomplete picture. Jerison (1973) has shown that cranial capacity of both predators and prey increased from the late Tertiary to the present, but it should be noted that brain size could have increased for reasons that have nothing to do with predation. Thus any proposed examples of predator-prey coevolution should be examined with caution. Furthermore, where behavioral adaptations are involved, statements about coevolution without the backing of an established phylogenetic history are likely to be received with skepticism.

That does not mean, however, that one cannot generate working hypotheses in an attempt to understand what might have happened. One can find support for the argument that birds and the cryptic insects they feed upon constitute an example of an evolutionary arms race (Dawkins & Krebs, 1979). When the body of an insect is similar in color and pattern to the background that it rests upon, a bird is less likely to be able to detect it (Pietrewicz & Kamil, 1977). The crypticity of such an insect, so the argument goes, is a direct result of the selection pressure they face from predators (Sargent, 1981). To counter the high degree of crypsis, birds may use searching images (Pietrewics & Kamil, 1981). That is, once birds learn what pattern to look for in a prey item, they can use that "searching image" to find more prey items of the same type. Over many generations, insect species may counter predator use of searching images by becoming polymorphic. A polymorphism is beneficial to a prey item because predators that have a search image for only one morph will overlook those of another type.

Maintenance of Polymorphisms:

While it may not be clear exactly how polymormphic populations came to exist, there is considerable evidence that they can be maintained by predators hunting by searching image. Birds utilize a searching image for the most common prey type, resulting in negative frequency dependent selection. While numbers of the more common morph decline from predation, individuals of the other type are overlooked and allowed to increase in numbers. Consequently two or more morphs may be maintained in a population through apostatic selection, because predators tend to utilize a search image for only the most common prey type.

The term "searching image" was originally used by Luc Tinbergen (1960). He conducted a study in a plantation of Scots Pine, in the Netherlands. He obtained insect density measurements by counting insects in twig samples and by counting insect faecal pellets. Simultaneously, he observed the food great tits (*Parus major*) brought back to glass-backed nestboxes which were attached to a hide. Based on what he knew was available to the birds and what he saw the birds were actually taking, he examined the relationship between the density of different prey species and the composition of the food brought to the nest of great tits. He found that when a species was relatively uncommon, the percentage of that species in the food taken to the nest was quite low. At slightly higher densities a much larger number of items of that species was taken than predicted by the expectation curves; thus the predators effectively over-selected the food type of the highest density. Tinbergen explained that searching images are adopted only when a prey type has exceeded a certain density, for the birds would need to make a limited number of chance encounters with the cryptic prey prior to acquiring the search image. At higher densities, predators would become more efficient.

Although Tinbergen's paper made compelling arguments, there have always been alternative reasons why a predator might collect groups of a more common prey type. For example, Coppinger (1970) found that adult blue jays, taken from the nest prior to fledging, do not immediately attack novel insects such as mealworms or butterflies: the prey are obviously conspicuous, so they do not need to learn to identify them. Learning that they may be eaten, however, takes time, and this is more likely to happen when they are found in high densities.

Alternatively, predators may have to learn to capture common prey. Recher &

Recher (1969) observed that juvenile reef herons (*Egretta sacra*) in Queensland Australia, "capture less food per minute and miss more frequently" than adults in the same area. Thus it may be argued that learning to handle some prey types takes time, and predators are more likely to learn to handle those that are numerous.

Another possibility is that predators do not just learn what prey look like, but where to go to find abundant prey. For example, Dixon (1959) studied the searching behavior of the coccinellid beetle *Adalia decumpuctata* and found that larva do not move at random over the surface of a leaf, but follow irregularities such as the veins or rim, and since nettle aphids are likely to be found in these locations, the behavior of the beetle increases its chances of finding them. In addition, Dixon found that when larvae encounter aphids, they turn, so when aphid densities are high, they confine themselves to a smaller area and maximize chances of finding more prey. Consequently, if prey items are clumped, such a predator is likely to encounter a large number of the same type of prey.

Some predators seem to be particularly sensitive to prey density. Smith & Dawkins (1971), following the work of Royama (1970), found that individual great tits *Parus major* spend a large proportion of their time searching in regions that have the highest food density. Finally, Krebs et al. (1972) found, in rather artificial conditions, that when great tits find a food item in a particular place, they "switch on" to looking in that type of place over the next few minutes. Thus birds may not only pay particular attention to what to look for, but where they should look for it.

Recent Searching Image Studies:

Given that apostatic selection, and polymorphism, may result from a variety of mechanisms other than hunting by searching image, more recent studies have been more restrictive. For example, in order to eliminate the possibility that some prey items would be taken at a greater rate due to palatability or handling time differences, Marian Dawkins (1971) presented domestic chicks with colored rice grains. To manipulate crypticity, she manipulated the background. When the background was the same color as the rice, the birds pecked at the background stones at first, but after three or four minutes they started to find the grains and soon were finding them at the same rate as in the treatment in which they appeared on backgrounds that made them conspicuous. The birds "learned to see" the cryptic prey. A similar effect was observed by Gendron (1986) when bobwhite quail were presented with green pellets on a brown background following feeding on brown pellets. Although they had eaten such green pellets in the past, "it was not until the second trial of the third day that all of the birds appeared to find the pellets without any trouble" (p. 910).

One limitation of studies of granivorous birds feeding on seeds of various colors is that the proportion of each type of seed is changed as the bird feeds. Because the searching image is influenced by this ratio (Bond, 1983), observations of feeding behavior must either be short or incorporate the changing frequency of the prey types. Alternatively, prey items may be presented to a predator in the form of a choice test. In a choice test, the predator is presented with a background that either contains a prey item or does not, and the predator is rewarded for correctly making this determination. Such choice tests can easily be presented in an operant conditioning setup and were originally used by Herrnstein (1964) to study the ability of pigeons to respond to the presence or absence of human beings in photographs. If the bird looking at artificial presentations correctly detects a target item, it is given a real food reward. If it correctly determines that there is no target item, it can quickly move on to the next presentation. If it makes a mistake, it is punished with no food reward and a time delay before the next trial. In this procedure, the experimenter has complete control of the frequency and order in which the predator encounters prey.

In theory, if the predator is presented with only one type of prey (a "run" of one prey type) in such a procedure, the formation of a searching image is facilitated, and the performance of the bird will improve relative to a treatment in which the sequence of prey types presented is random (a "non-run"). Pietrewicz and Kamil obtained these results when they presented slides of *Catocala* moths resting on the bark of trees to blue jays in operant boxes (1977, 1979).

Despite this support, Guilford and Dawkins (1987) claimed that efforts to demonstrate that performance improved as a result of a perceptual change were flawed. They argued that the findings of these studies also supported the hypothesis that predators adjusted their search rate to compensate for the crypticity of their prey. They insisted that the initial inability of Gendron's bobwhite quail to find green prey (1986) was really the result of the birds being presented with familiar prey in an unfamiliar context. They claimed that Gendron's finding that the birds were able to find prey more quickly after sufficient exposure was not the result of learning what to look for, but of learning to slow their search rate to find the more cryptic food. Because Pietrewicz and Kamil (1979) had not published their latency data (except in the dissertation of Pietrewicz), Guilford and Dawkins went on to argue that the operant preparation may have failed to show searching images for the same reason. That is, if one prey type was more cryptic, the birds would consistently find that type only if they looked at the presentation long enough to find it. If they looked at the screen only as long as necessary to find the less cryptic type before giving up, they would overlook the more cryptic type. A run of the more cryptic type could train the birds to take more time and search the presentation more carefully, resulting in an increase in performance.

In addition to the reaction time data in Pietrewicz's dissertation (1979), the best counter-argument to the "search rate" hypothesis may be the results of a study by Reid and Shettleworth (1992), which deliberately used two equally cryptic prey types. After a series of exposures to a single prey type, predators were simultaneously exposed to both types of prey. They found that the birds preferentially pecked at the prey type used in the initial run, evidence consistent with the search image hypothesis.

Current Experiments:

While birds may also adjust search rates, there is considerable support for the hypothesis that birds use searching images, and it seems reasonable to begin to take advantage of the flexibility and control over stimuli appearance that operant tests provide. Rather than looking at projected images from photographs of moths pinned to trees, birds in operant experiments now see images presented on computer screens and their responses are detected by touchscreens (Bond & Kamil, 1998, 1999). Backgrounds or prey items can be manipulated at will to make prey easier or more difficult to detect. Furthermore, prey items can be manipulated to appear different from the images from which they were derived. This may make it possible to ask a variety of new questions. For example: How different in appearance does a rare morph have to be from a common morph to gain a selective advantage? It has been shown that if polymorphism occurs, and a predator uses searching images to detect its prey, it will often overlook a rare morph. Thus a rare morph has a selective advantage. But until now experimenters have always used very distinct looking morphs. Are subtle differences enough to confer a selective advantage, or must a mutation cause dramatic differences to be beneficial? By varying the degree to which two morphs resemble one another and presenting runs and nonruns, one may determine how polymorphisms may arise. This is the goal of the experiment described in chapter 2

Similarly, an effort should be made to investigate the effects of the inter-prey interval in an operant setting. A study by Plaisted (1997) made note of the fact that when birds face multiple presentations of a single prey type in an operant box, the time that elapses between presentations of that particular prey type is much shorter than when presentations of that type are interspersed at random with another prey type. As a consequence, a decrease in performance under the non-runs treatment relative to the runs treatment may be due to either an interference effect of one prey type on another or to a sort of memory decay. In her study with pigeons, Plaisted found no difference in performance when comparing runs treatments with long interstimulus intervals and non-runs treatments with normal interstimulus intervals. It is not clear whether this finding can be attributed to differences between Plaisted's methods and those used in other labs, or if similar findings might also apply to birds whose prey items are more likely to be widely dispersed in their natural environment. A post hoc analysis by Bond & Kamil (1999) suggests that runs effects persist for at least three minutes in blue jays using their lab preparations, compared to the decline after 20 seconds in Plaisted's study, but the point at which the inter-prey interval really begins to play a role is unknown. An explicit test therefore seems warranted, and this experiment is the subject of chapter 3.

Other manipulations of prey appearance may also be of interest. For example, Julesz (1969) found that humans readily detect patterns of symmetry in random dot patterns, suggesting that symmetry might be a salient cue for detection of cryptic (but bilaterally symmetric) prey. Formation of a searching image for such a prey item may also be facilitated because one half of the image is redundant with the other half, thus essentially half as much information must be retained in memory (Locher & Nodine, 1973). Whether, in the eyes of a bird, moths with asymmetric wing patterns appear more cryptic on bark backgrounds than symmetric moths has never been tested, because naturally occurring moths are highly symmetric. Using computer manipulated prey images, however, such tests could easily be done. If asymmetric moths are less conspicuous, it raises questions about what sorts of evolutionary constraints prevent the evolution of asymmetric wing patterns. Is symmetry important for mate attraction (Moller & Pomiankowski, 1993) in *Catocala* moths, despite the fact that they attract mates through pheromones? If symmetric moths are not easier to detect, why not?

Biederman (1987) has argued that the visual system should be especially sensitive to such non-accidental image properties. Are cryptic patterns enough to conceal symmetry? Chapter 4 is an attempt to address these questions.

CHAPTER 2: MANIPULATED POLYMORPHISM

INTRODUCTION

Tinbergen (1960) noted that insectivorous birds tend to take prey items in sequential runs, suggesting that they are only searching for one type of prey. By learning what to look for in a common but cryptic prey type, birds can more efficiently find and obtain additional prey items of that type. That is, they can utilize a searching image. The benefits of searching for a single prey type would be reduced, however, in locations in which prey are polymorphic, because a bird utilizing a searching image may overlook prey items of alternative phenotypes. It is therefore possible that because a morph is more likely to be overlooked by a predator utilizing a search image for a distinctly different morph, predation may drive the initial evolution of polymorphism or drive polymorphic populations to increased phenotypic dissimilarity (Bond & Kamil 1998).

The manner in which predation might influence the evolution of new phenotypes in a population is unclear. If a genetic mutation arose producing an individual that differed in phenotype from the majority of the population, such an individual might have a fitness advantage. That is, such an individual might lack the characteristics used by its predators to identify prey. If the changes in appearance are slight, however, the predator may still successfully identify the new prey item. Such an individual would be no more likely to pass on the genes for the new phenotype than any other individual in the population, and the mutation would be unlikely to spread to allow the new morph to become established in the population, unless it increased in frequency due to genetic drift.

Hence, successful new morphs are likely to differ substantially in appearance from existing forms.

Changes in appearance that make an individual appear different from its conspecifics may also have effects on crypticity, however. Many mutations will be unlikely to produce a lasting polymorphism because these individuals will not be cryptic and consequently will be easily detected by predators. Previous studies have shown that conspicuous prey items are unlikely to be overlooked, even by a predator that has previously been utilizing a searching image to detect more cryptic prey (Blough, 1989; Bond & Kamil, 1999).

The purpose in this experiment was to begin to investigate the potential importance of degree of resemblance between morphs on predator searching success, and thus its potential fitness consequences for prey populations. This was done by building upon the operant analogue to sequential prey captures developed by Pietrewicz and Kamil (1977, 1979, 1981). Their experiments utilized photographs of either of two moth types on tree bark, or photographs of tree bark with no moths present, and the presentation of each photograph corresponded to a predation opportunity. The sequence of images could be controlled to produce runs of a single prey type, or the two prey types could be randomly intermixed. Birds in these experiments showed increasing levels of accuracy and decreasing response times, with experience, during runs conditions, but not during non-runs. That is, in runs conditions, moths in the photographs were detected more quickly and accurately at the end of a series of like photographs than at the beginning, but little or no improvement occurred during the course of a session when trials were a random mixture of either moth type presented. The slopes of accuracy or detection time over the number of prior correct detections within a block of trials may be used as a measure of the additional cognitive demands required when searching for polymorphic rather than monomorphic prey.

To investigate whether the cognitive demands of searching for cryptic prey are greater when there is a polymorphism for more disparate appearing morphs, computer graphics files were generated from photographs to manipulate existing morphs to varying degrees to create new polymorphic populations. Complex backgrounds were then created through a process which could be manipulated to control the degree of crypticity of the moths. The effects of the differences in appearance between moths were investigated by presenting the moths on complex backgrounds, interspersed with trials containing backgrounds only, in controlled sequences of runs and non-runs.

METHODS

Subjects:

Six blue jays (*Cyanocitta cristata*), collected as fledglings and reared in the lab, from 6 to 16 years of age, were used as predators. Prior to the experiment, all six had been used in other operant studies requiring them to search for cryptic stimuli that differed in appearance from those used here. All were maintained at 80-85% of their free-feeding weight in individual cages on a 14:10 light:dark cycle, and training and experimental trials were conducted between 7 am and 4 pm.

Stimuli:

Prototype moth images were created by photographing preserved specimens of moths and converting the pictures to computer graphics files via a scanner and digital image editing software. Images were adjusted for symmetry, and wing position was manipulated slightly so that the moths appeared as they would in their normal resting positions. Size of the images was then reduced so that the images were 16 pixels tall and wide at Super VGA resolution (640 x 480), and the color was translated to greyscale with each pixel having a greyscale value ranging from 1 to 128.

From three greyscale moth images created directly from photographs, additional images were created by manipulating the prototype images to varying degrees. For each prototype moth, three additional moths were generated in which 20%, 40%, or 80% of the pixels in the image were manipulated for greyscale value. To avoid changes in overall light intensity of the moths as changes were made, changes were made in pixel pairs. Two different pixel locations were chosen at random, and the greyscale value at one location was switched with the greyscale value at the other location. In an attempt to produce patterns on the wings of manipulated moths that were roughly similar (to human eyes) to those on natural moths, an additional constraint was added: if a greyscale value at a given location was set to be changed to a value more than 10 shades different from any of its 8 nearest neighbors, two different pixel locations were chosen. Essentially this promoted clustering of pixels of similar intensity. Consequently, the manipulated moths differed from the originals in pattern, but not in either shape or the frequency distribution of greyscale values (Figure 2A).

Backgrounds:

Backgrounds for producing varying degrees of moth crypticity were created by an algorithm for selecting a greyscale value for each pixel in the rectangular field. The moths appeared most cryptic on a background generated from selecting pixel greyscale values from a frequency distribution identical to the combined frequency distribution of the three prototype moths. To create varying levels of crypticity, backgrounds were created by combining different percentages of pixels from the combined moth image frequency distribution and from a uniform grey-scale distribution. A background of level two was created from 20% of the moth pool, level three from 30%, and so on. Manipulating the proportion of background pixels selected from each distribution indirectly controlled the difficulty with which the birds were able to detect moth images. In order to quickly present new backgrounds for each session, new backgrounds were generated and saved as large graphics files between testing sessions.

Apparatus:

The birds were tested in a 52 cm high x 36 cm wide x 62 cm long galvanized steel operant box (Figure 2B). A touch screen (Carroll Touch Smart Frame), which detected the location of pecks at stimuli was located within the operant chamber and within 2 cm of the face of the monitor. A piece of plexiglass mounted on foam pads near the screen of the monitor reduced the impacts of the pecks on the beaks of the birds. A speaker for a white noise generator was positioned on one side, to reduce distractions from outside noise, and an overhead light was positioned above the monitor to illuminate the perch. A perch was positioned so that it was at the same height as the bottom of the monitor screen and 12 cm from the plexiglass. An opening in the floor of the operant box, beneath the perch, allowed the birds to reach and retrieve food rewards. These food rewards were delivered by a lazy suzan style feeder.

Procedure-

Pretraining:

After habituation to the operant box, the birds were trained to eat from the food well as it provided rewards at random time intervals, a process called magazine training. Next, each blue jays was "hand-shaped" to peck at moth stimuli visible in a fixed position on the computer monitor. The experimenter carefully watched the bird in the operant box and advanced the feeder as the bird made progress towards pecking moths. Initially, food rewards were provided when birds merely looked at these stimuli, and were later only provided when the birds pecked at the images. Moth images were the same size and shape as those used during testing, but for training purposes were presented on a neutral gray background so that they were quite easy to see. When the birds were consistently pecking at the moths on the screen for rewards, the hand-shaping stage was complete, and the touchscreen and computer were used to detect pecks and provide rewards.

After the birds learned to peck at moth images for food rewards, they were trained to peck at a red circle in the middle of the monitor screen. This peck at the 'start key' started the next phase of the trial: The red circle disappeared and was replaced by the image of the moth. When the bird pecked within 2 cm of the center of this moth image, a food reward was delivered. The start key procedure was used to allow the bird to start each trial, which reduced the variability of latency measures.

In the next stage, the location of the moth images on the screen varied at random from trial to trial, so birds were required to search the entire screen and peck at the correct position during each trial. Once the birds had learned to do this, the difficulty of detecting the moth image was increased by introducing more cryptic backgrounds. Moths were initially presented on backgrounds of difficulty level one (10% of the pixel greyscale values were identical in frequency distribution to those of the moths, and 90% were from a uniform grey-scale distribution), which made the moths easily detectable, yet more difficult than finding the moths on an essentially empty background.

Next, a green circle in the center of the screen which accompanied moth images (the 'giving up' key) was introduced. Birds were not rewarded with food for pecking at the green circle, but instead were immediately presented with a new start key screen. Next, birds were subjected to trials in which the green key was presented along with backgrounds containing no moth. In these trials, pecking the background at random caused the screen to go black, and the birds were forced to wait for 50 seconds before seeing the start key again. Pecking at the green circle, however, reduced the time between trials to 3 seconds. If the bird refused to peck at anything, the screen went black after 60 seconds, and the bird was forced to wait an additional 12 seconds between trials.

Training:

After the bird successfully learned to peck at more than 90% of the moths when present, and the green circle on more than 90% of trials when moths were absent, backgrounds were adjusted so that moths became much more difficult to detect. During training before each test stage, each bird was presented with two moth types, one a prototype, and the other a manipulation of the prototype, each of which appeared in 25% of the trials. The remaining 50% of trials were "negative" trials, in which there was no moth present, and the correct response was to peck at the green circle.

When the birds were responding to negatives correctly for more than 90% of trials and to the more difficult of the two positive stimuli for 70-80% of trials for four or more consecutive days, the testing phase began. Although moths manipulated 20% or 40% were similar in crypticity to unmanipulated moths on the generated backgrounds, those moths that were made more disparate in appearance were more easily detected, hence the background was adjusted to control the detection rates of only the more difficult moths. To reach this goal, detection rates were monitored daily during training. When birds exceeded 80% detection for more than one day, the background difficulty was increased. When performance fell below 70% detection for two or more consecutive days, the background difficulty level was reduced.

Testing:

For each moth-pair difference treatment, birds were tested for 12 days. Each day of testing, the birds were exposed to 36 positives and 36 negative trials. Within each 72 trial session there were three blocks of 16 test trials. The first treatment block was randomly positioned following 5 to 7 warm-up trials. The third block of the session was positioned so that the end of the block was within 3 trials of the end of the session. The second block was randomly positioned between the first and third blocks, with at least 5 trials separating treatment blocks.

In one treatment block, the eight positive trials were a randomly ordered presentation of four moths of each type, along with an equal number of interspersed negative trials. This was the "non-run" condition. In the other two blocks, the eight positive trials contained only a single moth type, interspersed with eight negative trials. These were the two "runs" conditions. The order in which the three block types were presented each day was randomized, and the starting points of the test blocks within the 72 trial session were shifted randomly each day. "Warmup" trials, and trials between test blocks were 50% negative, with the two moth types equally represented in the positive trials. For each trial, the trial type, response of the bird, and reaction time were recorded for analysis.

Analysis:

The effects of the number of prior detected targets were used to analyze stimulus sequence effects. This measure adjusts for the actual prior experience of the subject with the moths in the block (Kono et al, 1998). This measure was then reduced to a two-level category variable termed NPD (for number of prior detections). Accuracy and reaction time on trials following 2 or fewer prior detections were compared with trials following 3 or more prior detections.

Accuracy was calculated based on the percentage correct responses for each combination of bird, stimulus type, and NPD, separately for trials with and without moths. Reaction time for correct detection of moths was calculated based on the average response time for each bird, stimulus type, and NPD combination.

RESULTS

Positive and Negative Trials:

The birds responded correctly more often when moths were absent than when they were present. Mean accuracy was 76.6% on positive trials and 97.7% on negative trials, $F(1,5) = 114.29$, $P < 0.001$. When the birds responded correctly, they required less time to detect moths (11.4 s) than to peck the giving-up key (20.6 s), $F(1,5) = 66.39$, $P < 0.001$. When the birds failed to detect moths, they usually pecked at the giving-up key; only 5.4% of errors on positive trials were pecks at incorrect positions on the background.

Sequence Effects-

Time to Detect Prey During Runs Sessions:

The purpose of these analyses was to examine the effects of runs of a single prey type on how quickly the jays were able to find prey. Data from the runs trials during which the jays correctly detected a moth target were analyzed with an NPD x moth pair difference x bird ANOVA. Latencies greater than 20 s (less than 7% of trials) were truncated to 20 s to avoid a few very long latencies from skewing the data. Jays responded fastest when moths were 80% different (5.8 s) as compared to when they were either 20% (8.8 s) or 40% (9.1 s) different, resulting in a significant main effect of moth pair difference, $F(2,10) = 7.82$, $P < 0.01$. Neither the effects of NPD, $F(1,10) = 2.59$, $P < 0.20$, nor the interaction of NPD with pair difference, $F(2,10) < 1$, was significant.

Accuracy for Positive Trials in Runs Sessions:

The purpose of these analyses was to examine the effects of runs on how accurately the jays detected prey. Data from experimental blocks that included runs of a single prey type were analyzed with an NPD x moth pair difference by bird ANOVA. Jays were most accurate when moths were 80% different (82.1%), as compared to when they were either 20% (75.8%) or 40% (71.8%) different, resulting in a significant main effect of moth pair difference, $F(2,10) = 4.69$, $P< 0.05$. While accuracy increased with NPD for all three treatment groups, $F(1,5) = 166.4$, $P < 0.001$, it increased most dramatically for the 40% difference group (Figure 2C), resulting in a significant moth difference x NPD interaction, $F(2,10) = 6.99$, $P < 0.05$. In order to explore this interaction, data from each pair difference treatment was analyzed separately with bird x NPD x moth ANOVAs.

The purpose of utilizing moth type as a factor was to examine whether the increase in accuracy with NPD was influenced by the appearance of the two moth images viewed by a bird in a session. While the moths were made to resemble one another to varying degrees, the differences in methods used to generate the two moth images might influence crypticity and, consequently, accuracy. There was no effect of moth type in the 20% or 40% difference group, $F(1,5) < 1$, but the effect of moth type in the 80% difference treatment group (figure 2D) was highly significant, $F(1,5) = 166.90$, $P < 0.001$. In the 80% difference treatment group, the parental strain moths, the images simply reduced in size from the photographs of a moth, were quite cryptic in comparison to the mutant strain. Only for the more cryptic moth type was there an effect of NPD. Average accuracy for the parental strain moths increased with NPD, from 62.8% to 76.5%, while average accuracy for the mutant strain moths only increased from 95.1% to 96.2%, resulting in a significant NPD x moth type interaction, $F(1,5) = 8.77$, $P < 0.05$.

Accuracy for Negative Trials in Runs Sessions:

The purpose of these analyses was to examine the effects of runs on how accurately the jays detected the absence of prey. Data from non-moth trials in experimental blocks that included runs of a single prey type were analyzed with an NPD x moth pair difference by bird ANOVA. There was not a significant main effect of moth difference, $F(2,10) < 1$, as jays were most accurate when moths were 80% different (98.4%) but also quite accurate when moths were 20% (97.6%) or 40% (97.3%) different. While accuracy on no-moth trials increased an average of 1.3% following 3 or more prior moth detections, compared to 2 or fewer, there was not a significant effect of NPD. $F(1,5)$

< 1 , nor was there a significant moth difference x NPD interaction, F(2,10) < 1.

Runs vs. Non-Runs:

If the effects of runs on detection accuracy were the result of repeated encounters with a single moth type, accuracy should increase more than when moths were presented in random order. To compare runs and non-runs treatments, each moth difference group was subjected to a separate sequence type (run vs. non-run) x NPD by bird ANOVA. Average accuracy was found to be slightly higher under runs conditions than during non-runs conditions when moths were 20% or 40% different (Figure 2E). However, these differences were not significant, F(1,5) < 1. While the increase in accuracy with NPD was not significant for the 20% difference group, there was a significant main effect of NPD for both the 40% group, F(1,5) = 129.79, P < 0.001, and the 80% group, F(1,5) = 33.8, P < 0.01. Because these increases in accuracy occurred regardless of sequence type, however, there were no significant NPD x sequence type interactions, F(1,5) < 1.

In the 80% difference group, but not in the others, mutant strain morphs (moth images deliberately manipulated by pixel-swapping) appeared more conspicuous to the birds than did the parental strain morphs. Consequently, there might be an NPD x sequence type interaction for one moth type, but not for the other.

To test the hypothesis that there was a runs effect for only one moth type in the 80% treatment group, accuracy for each moth during runs and non-runs was compared in separate three-way repeated measures ANOVAs (bird x NPD x sequence type). In the comparison of accuracy for parental strain moths in runs and non-runs (Figure 2F), there was an overall significant increase in accuracy, F(1,5) = 11.42, P < 0.001, but no significant NPD x sequence type interaction, F(1,5) < 1. Although average accuracy during runs was 61% compared to 69% for non-runs, there was also no significant effect of sequence type on overall accuracy, F(1,5) < 1.

There were no differences in the comparison of accuracy during runs and non-runs of mutant strain moths. Average accuracy was 95% during non-runs and 96% during runs, and there was not a significant main effect of sequence type, F(1,5) < 1. Accuracy increased only slightly from 92% to 97% during non-runs, and remained at 96% during runs (Figure 2G). Thus, there was not a significant main effect of NPD, F(1,5) < 1, and there was no NPD x sequence type interaction, F(1,5) < 1. Average accuracy for either moth type was similar for both runs and non-runs treatments, and any increase in accuracy as a result of number of prior detections was similar, regardless of presentation sequence.

Test Block Order Effects:

In the 40% difference treatment group, a significant NPD effect was detected, but there was no NPD x sequence type interaction. This pattern deserves additional consideration. One factor that might cause poor performance for one moth type early in a non-runs treatment block is recent experience within a runs treatment block. To test this hypothesis, data for non-runs from the 40% treatment group were categorized according to treatment order. Non-runs blocks either followed a runs block or preceded all runs. The data was subjected to a three-way repeated measures ANOVA (bird x NPD x order).

Average accuracy in non-runs blocks was 71.0% following runs treatments and 71.2% when the non-runs treatment was first in the session, $F(1,5) = 8.42$, $P < 0.05$. While the means were the same, accuracy in non-runs blocks started lowest and ended highest when the blocks followed runs treatment blocks. After a run of one moth type, the average accuracy in non-runs treatment blocks increased with NPD from 66.0% to 79.1%, while accuracy in non-runs blocks that were the first treatments in daily sessions actually decreased slightly 71.5% to 70.8% (Figure 2H), resulting in a significant NPD by sequence treatment order interaction $F(2,10) = 13.63$, $P < .05$. A subsequent planned comparison found no significant difference in accuracy due to treatment order in trials following 0, 1, or 2 prior detections, $t(5) = 1.80$, $P = 0.13$. However, a significant difference in accuracy due to treatment order was found for accuracy following 3 or more prior detections, $t(5) = 2.78$, $P = 0.04$.

Runs vs. Non-Runs Utilizing Data from First Test Blocks of Daily Sessions:

In the early study by Pietrewicz and Kamil (1981), non-runs treatment blocks were embedded in separate sessions, with at least 90 minutes separating sessions. In this study, non-runs treatment blocks frequently followed runs treatment blocks separated by only an average of 10 buffer trials. In an attempt to replicate the conditions of the Pietrewicz and Kamil study using this data set, all data following the first treatment block for each daily test session were removed, thus removing any short-term carryover effects. Data from both runs and non-runs treatments from the 40% difference treatment group were subjected to a NPD x sequence type (run vs. non-run) by bird ANOVA. For the runs treatment group, accuracy increased from 64.9% to 80.0% while accuracy decreased slightly during non-runs from 71.5% to 70.8% (Figure 2I), resulting in a significant NPD x sequence type interaction, F(1,5)=6.97, P<.05, suggesting that there is a searching image effect under the 40% moth difference condition.

Finding a searching image effect for one treatment group using a reduced data set raises questions about whether such effects were also present for the other treatment groups. To test the hypothesis that there are searching image effects in the first treatment blocks of the data from the 20% moth difference group, the same procedure was used to extract the appropriate data. Data from the first treatment blocks were subjected to a NPD x sequence type by bird ANOVA. Birds performed only slightly better during runs treatment blocks, averaging 77.3% correct, compared to 75.5% correct during non-runs. Consequently, there was not a significant main effect of sequence type, F(1,5) < 1. Accuracy increased from 71.8% to 82.9% during runs, but quite similarly increased from 69.5% to 81.4% during non-runs (Figure 2J). Thus, there was not a significant NPD x sequence type interaction, F(1,5) < 1. There was not a significant runs effect greater than that observed when moth presentation sequence was random for the 20% moth difference group.

The same procedure was used to test the 80% moth difference treatment group. Accuracy was slightly higher during runs, averaging 84.3% compared to 77.5% for non-runs, but there was not a significant main effect of sequence type, F(1,5) < 1. Accuracy also increased with number of prior detections during runs treatments, climbing from 80.6% to 88.1%. This increase was equivalent to performance in the non-runs treatment condition, where accuracy increased from 70.7% to 84.2% on average (Figure 2K). Although there was a significant main effect of NPD, $F(1,5) = 7.04$, $P < 0.05$, the NPD x sequence type interaction was not significant, $F(1,5) < 1$.

When data from all treatment blocks for the 80% difference group were examined, there was a significant effect of moth type, due to higher crypticity of the prototype moths. To determine if this effect was present during the first blocks of the session. the appropriate data was subjected to a NPD x moth type x sequence type by bird ANOVA. Accuracy for the prototype was much lower than for the manipulated moth, $F(1,5) = 26.77$, $P < 0.01$.

DISCUSSION

There are two important results of this study. First the degree of resemblance between moth types had significant effects on the use of searching images. Responses of birds preying upon moths that were 20% different were not the same as for birds preying upon moths that were 40% different, and predation on moths that were 80% different produced unique results as well. Second, this is the first study to examine behavior of birds in non-runs treatment blocks following a series of trials in which only one moth type was present. When non-runs blocks were the second or third treatment blocks of a daily session, following at least one runs block, accuracy was initially poor. This suggests that the birds continued to search only for the target-type found in the previous runs block. However, after three or more detections within the block, accuracy was quite high, relative to accuracy in non-runs blocks that were first treatment blocks in daily sessions.

Degrees of Prey Resemblance and the Searching Image:

Many studies suggest that polymorphism could be maintained by predators that concentrate on the most common morph, neglecting rarer ones (Poulton, 1884; Tinbergen, 1960; Clarke, 1962; Allen & Clarke, 1984; Allen, Raymond, & Geburtig, 1988, Glanville & Allen, 1997; Bond & Kamil, 1998). The question of how polymorphism initially occurs in nature, however, is more difficult to address because the morph frequencies are likely to already be in equilibrium, thus selection by the predators is difficult to detect (Allen, 1988). To begin to address this question, this study used artificial morphs and highly controlled conditions to determine how the degree of resemblance between artificial morphs influences the use of search images.

Search images are identified by runs effects, which are defined as the difference in performance between sequences containing only one moth type and sequences of two moth types presented in random order. Provided a moth is sufficiently cryptic (Blough, 1989), and provided the birds have not had too much experience with the prey type (Kono et al, 1998), the birds can use a searching image to increase their performance with experience during runs blocks. During non-runs, where two prey types are similar. birds can also develop and use a searching image to increase performance, because experience in detection of one moth type can enhance the ability to detect the other. In contrast, when the two prey types are distinctly different, conditions during non-runs do not favor the use of a searching image, because a bird utilizing one searching image may overlook prey of the other type. To maximize efficiency, therefore, birds are expected to search more generally, producing little or no increase in performance with experience.

This study provides support for these hypotheses. In the 20% difference group, moths resembled one another much more than in the 40% difference group. While there was a significant sequence type (run vs. non-run) by NPD interaction for the 40% difference group, there was no such effect for the 20% difference group, where birds showed similar levels of improvement with experience, regardless of sequence type.

If moths that are 40% different fall into distinctly different searching images, moths that are 80% different might be expected to require separate searching images as well. A test of runs and non-runs performance of birds searching for two moths types differentiated by 80% of their pixels, suggested that the issue is more complicated. Average accuracy increased with experience in the 80% difference group, both during runs and during non-runs.

Crypticity differences of the two moth types may be responsible for the general increase in performance across both runs and non-runs for the 80% difference moth pair group. Swapping pixel greyscale values at random locations on the moth image made the manipulated moths look less like their prototype. However, with extreme changes. it also produced patterns that the birds were able to differentiate from the background. While mean accuracy for the moth pair increased 7.4% during runs, and 13.5% during non-runs, the changes in accuracy really only applied to one of the moths. The greatest increase in accuracy for the manipulated moth was a change during non-runs from 94.2% to 95.5%. That is, performance improved for the more cryptic moth under both runs and non-runs conditions, while accuracy for the manipulated moth remained high, regardless of sequence type. The results, then, are consistent with the use of a searching image for only the prototype moth. A bird may be able to utilize a searching image for the cryptic moth, regardless of sequence type, to increase accuracy with increasing numbers of prior detections.

These findings have important implications for the relationship between moths and avian predators outside the laboratory. First, a failure to demonstrate differences between runs and non-runs treatments in the 20% difference group suggests that genetic mutations that produce small changes in wing pattern may be insufficient to protect a moth from a predator utilizing a searching image for the parental-type wing pattern. Gilbert (1983) has found that single gene substitutions often produce qualitatively different color patterns in *Heliconius* butterflies, and these sorts of changes may be more likely to offer protection and produce polymorphic populations.

However, the high predation rates on the manipulated morph in the 80% difference group, despite the apparent use of a searching image for the prototype morph, suggests that a moth that does not fit a given search image is not necessarily protected. A mutation that results in an extreme phenotypic change may greatly diminish crypticity on a given background. It should be noted, however, that alternative substrates are likely to be available, and mutant individuals are under great selective pressure to select alternative resting sites. Different morphs of the species *Catocala* tend to be found on different species of tree, for example (Sargent, 1981).

Effects on Non-Runs Following Runs Treatments:

During runs treatment blocks, birds are expected to develop and utilize a searching image for the moth type that is present. Once the blocks end, birds are expected to abandon the searching image in favor of a more general searching strategy to maximize their rate of food intake. This transition from runs to non-runs has not been studied nearly as extensively as the non-runs to runs transition. Questions about how much time the transition should take, or for how many unprofitable trials a bird should continue to use a searching image have remained unanswered. The results of this study suggest that birds may continue to search for a single prey-type through ten or more non-runs trials.

When non-runs treatments followed runs treatments, mean accuracy was 6% lower following two or fewer prior detections than when non-runs treatment blocks were the first blocks of the session. While this difference was not statistically significant in this study, it suggests that the birds may have still been searching for only one moth type early in the block, producing an interference effect in detection of moths of the other type. Bond & Kamil (1999) found reduced accuracy in single probe trials following runs blocks of another type, but their results are based on single trials immediately following the run. The results in this study are based on several trials (accuracy following 0, 1, or 2 prior detections) in a block of trials, separated from the previous runs block by an average of 10 buffer trials.

A unique finding was that mean accuracy at the end of non-runs treatment blocks was significantly higher if the non-runs treatment followed a runs treatment. Mean accuracy following three or more prior detections was 9.5% higher when the non-runs treatment followed a runs treatment than when the non-runs treatment was the first block of the session. The birds were not only able to adjust their strategy to find the prey that they were missing early in these non-runs blocks, but they were able to find more moths at the end of the block than if they had not experienced runs earlier in the session. The birds may have been able to maintain the previous searching image while increasing their accuracy for the "new" targets. This might be related to the finding by Vreven and Blough (1998) that pigeons can process multiple memory items in parallel, to search for multiple targets simultaneously, provided they have enough experience with those targets.

These finding suggest that searching image effects are persistent. When non-runs treatment blocks were the first blocks in a session, there was no increase in performance, suggesting that birds did not use a searching image, but relied instead upon a more general searching strategy. In contrast, during non-runs blocks that followed runs blocks, accuracy was lower early in the block, and accuracy increased with increasing numbers of prior detection. Thus the use of a searching image earlier in the session influenced behavior even after 10 random buffer trials. This is in contrast with a study by Plaisted (1997), which suggests that searching images are short-lived under conditions in which there is not frequent reinforcement.

Conclusions:

In summary, the results suggest that when two prey types are very similar, both may fall into the same searching image. Consequently, an individual with a mutation for a small change in phenotype may be no more likely to pass on its genes than any other moth in a population. Larger changes in phenotype however can provide protection from the use of a predator's searching image, but only if the change results in a pattern as cryptic as other moths in the population. The results also suggest that runs treatments produce effects of longer duration than previously considered.

CHAPTER 3: INTER-PREY INTERVAL

INTRODUCTION

A number of different researchers, using a variety of techniques, have found support for the searching image hypothesis. Tinbergen (1960) coined the phrase "searching image" based on his observations of birds that over-selected frequently occurring cryptic insects and under-selected infrequently occurring ones. He believed that through an attentional mechanism, characteristics of the more frequent prey type were assimilated into a search image which allowed a predator to more efficiently find more of that type at the cost of being more likely to overlook insects that look different. Others have seen similar apostatic selection the field (Lawrence, 1985; Croze, 1970; Murton, 1971), or in open room experiments where birds feed upon cryptic seeds (Gendron, 1986; Dawkins, 1971) . To allow for experimental manipulation of the conditions under which the use of a searching image is likely to occur, researchers have also presented birds with trays of cryptic seeds (Bond, 1983; Ried & Shettleworth, 1992), projections of photographs that include cryptic prey (Pietrewicz & Kamil, 1979, 1981), or images on computer screens (Plaisted & Mackintosh, 1995; Blough, 1989; Bond & Kamil, 1999). The latter methods, which include only representations of food items, provide support for the hypothesis that their subjects utilize searching images by manipulating the sequence in which predators encounter prey. When birds are presented with a sequence of trials in which only one prey type is present, they find more of the cryptic prey items, and they find them more quickly, as they progress through the sequence. In contrast, performance in trial sequences in which multiple prey types are presented at random remains relatively constant, as the conditions are unfavorable for the use of a searching image strategy.

Plaisted (1997) has argued that although the results of such operant laboratory tests support the predictions of the searching image hypothesis, they support an alternative hypothesis as well. It may be that these animals are simply forgetful. In a session in which the birds are presented with a sequence of trials in which there is only one prey type present, the time that elapses between the presentation of one prey item and the next instance of that prey type is short. If, however, the session is one in which the prey types are mixed, the time that elapses between the successive presentations of any single prey type is increased. When the interval between the presentation of a given prey type and the subsequent presentation of the same prey type is short, there may be facilitation; birds could more quickly and easily find the next prey item. As the time interval increases, however, the memory for the appearance of the prey item begins to decay. Consequently, in a non-runs treatment session, the birds cannot remember what to look for, and performance is stagnant.

There is evidence to suggest that short term memory of pigeons is quite short (MacPhail, 1980; Roberts & Grant 1976; Roberts, 1972; Wagner, 1976). In delayed matching to sample tasks for example, pigeons have been presented with a colored key followed by a delay, then forced to choose correctly between two colored keys to obtain a food reward. The ability of the birds to remember the color of the sample key following the delay in order to peck the correct key is poor, and performance decreases with increasing delays (Roberts, 1972; Roberts & Grant, 1976). Remembering an arbitrary color, and remembering the pattern or shape of a cryptic food item, however, may be very different tasks. Perhaps the ability to remember the latter has been under greater evolutionary pressure.

Plaisted (1997) looked for effects of inter-stimulus interval using pigeons and an experimental design similar to that used by Pietrewicz & Kamil (1979), but unique in that she inserted additional 20 second delays between trials in runs and non-runs treatments on alternating days. While she found improvements in detection during runs with no additional delays inserted, she found that performance was no better in runs treatments with delays than during non-runs treatments with no additional delays. Degradation of short-term memory seems to be a reasonable explanation for this finding, and may be something to consider in evaluating the results of previous studies. On the other hand, there seem to be differences in her experimental design that make a direct comparison to previous studies difficult. For example, it appears that in an effort to generate stimuli of similar crypticity, backgrounds used for stimulus 1 were different than for stimulus 2. This could act as a priming device to let the birds know which prey type to look for during non-run trials.

More importantly, studies of the effects of elapsed time on searching behavior of blue jays do not seem to support Plaisted's hypothesis. Bond & Kamil (1999) found the main effect of interstimulus interval on accuracy was not significant, and while their data supported the hypothesis that interstimulus interval influences reaction time, there was actually a decrease in reaction time following delays. Overall, the inclusion of the interstimulus interval in the analyses did not remove the main effect of the number of previous detections.

Still, the issue of inter-prey intervals seems potentially important and largely ignored. If cryptic prey items are clustered, so that the birds capture several insects of the same type relatively quickly, increases in detection ability with experience may be greater than if each individual of the most common prey type is of considerable distance from others of its kind. Furthermore, it seems likely that both the distance to the nearest prey item and the overall density of a prey type are influenced by predation. Thus the likelihood of switching from one prey type to another may depend not only on relative frequency of prey types, but also on distance (and time spent) between prey items. Granted, a bird that encounters long delays between finding prey items may simply choose to leave such an unprofitable patch (Krebs, Ryan, & Charnov, 1974; Kamil, Yoerg, & Clements, 1988), yet the question remains: is a search image strategy likely to be maintained following a delay in which no prey of any kind are detected?

Additionally, it may be of interest to consider the potential for species differences between predators. It may be that because pigeons typically feed upon grains that are spread across the ground (Murton & Westwood, 1966), distance and time between the encounter of one food item and the next are quite limited. A blue jay, searching for moths on the bark of trees (Sargent, 1973), in contrast, is likely to require more time to find its next food item, and perhaps it retains a searching image for longer durations as well. Perhaps the differences in the findings of Plaisted (1997) and those of Bond and

Kamil (1999) are related to the differences in the selective pressures these birds face, and the subsequent differences in cognitive abilities of their subjects.

This research attempts to determine whether blue jays, provided with conditions that would ordinarily produce a runs effect, are influenced by either a 20 second or 60 second delay between two positive trials. Assuming that memory decay occurs in blue jays as Plaisted's research with pigeons suggests, any increase in prey detection performance up to the point at which the delay occurs is likely to be reduced, if not lost, following the delay. To test this hypotheses, birds were presented with stimulus arrays consisting of digitized moth images overlaid on complex backgrounds. Birds were exposed to treatment blocks of 32 trials, half of which were positive trials, each of which contained a moth image. The presence of a runs effect was established by comparing runs and non-runs treatment blocks, and the effects of delays on performance were investigated by introducing an additional delay between the 9th and 10th positive trials in half of those runs blocks.

METHODS

Subjects:

Six blue jays (*Cyanocitta cristata*), collected as fledglings and reared in the lab, from 2 to 6 years of age, were used as predators. Prior to the experiment, all six had been used in other operant studies requiring them to search for cryptic stimuli, but the stimuli differed in appearance from those used here. All were maintained at 80-85% of their free-feeding weight in individual cages on a 14:10 light:dark cycle, and training and experimental trials were conducted between 7 am and 4 pm.

Backgrounds:

Backgrounds were created by an algorithm for randomly selecting a greyscale value for each pixel in the rectangular field. To create varying levels of crypticity. backgrounds were created by combining different percentages of pixels from the combined moth image frequency distribution from the moths in a previous experiment and from a uniform grey-scale distribution. A background of level two was created by drawing 20% of the greyscale values from the moth pool and 80% from the uniform pool, level three by drawing 30% from the moth pool and 70% from the uniform pool, and so on. Manipulating the proportion of background pixels selected from each distribution indirectly controlled the difficulty with which the birds were able to detect moth images (Figure 3A). In order to quickly present new backgrounds for each session, new backgrounds were generated and saved as large graphics files between testing sessions.

Stimuli:

Moth images for this study were created by using the same algorithm that was used to create a background image of difficulty level six. Rather than using photographs of real moths, reducing their size, and then generating an algorithm to attempt to produce backgrounds upon which the two disparate moths were relatively equal in crypticity, moths for this study were generated to resemble the background (Figure 3B). For each moth, a block of pixels (8 wide x 16 high) was generated using the background generating algorithm. From this block, a mirror image was created to form a right half of the previously generated left half. Finally, this combined block (16 pixel high by 16 pixel wide) was shaped to form a more moth-like image by removing pixels from the upper corners and middle bottom region to create left and right halves that resembled the wings of a *Catocala* moth.

Apparatus:

The birds were tested in a 52 cm high x 36 cm wide x 62 cm long galvanized steel operant box. A touch screen, which detected the location of pecks at stimuli was located within the operant chamber and within 2 cm of the face of the monitor. A piece of plexiglass mounted on foam pads near the screen of the monitor reduced the impacts of the pecks on the beaks of the birds. A speaker for a white noise generator was positioned on one side, to reduce distractions from outside noise, and an overhead light was positioned above the monitor to illuminate the perch. A perch was positioned so that it was at the same height as the bottom of the monitor screen and 12 cm from the plexiglass. An opening in the floor of the operant box, beneath the perch, allowed the birds to reach and retrieve food rewards. These food rewards were delivered by a lazy suzan style feeder.

Procedure-

Pretraining:

After habituation to the operant box and magazine training, in which food rewards were provided at random time intervals, blue jays were hand-shaped to peck at the computer monitor by training them to associate pecking at conspicuous moth stimuli in a fixed position on the computer screen with a food reward. Moth images were the same size and shape as those used during testing, but for training purposes were presented on a neutral gray background so that they were quite easy to see. Initially, food rewards were provided when birds merely looked at these stimuli, and were later only provided when the birds pecked at the images.

After the birds learned to peck at moth images for food rewards, they were trained to peck at a red circle in the middle of the monitor screen which started the next phase of the trial. When pecked, the red circle disappeared and was replaced by the image of the moth. When the bird pecked within 2 cm of the center of this moth image, a food reward was delivered. The start key procedure was used to allow the bird to start each trial, which reduced the variability of latency measures.

In the next stage, the location of the moth images on the screen varied at random from trial to trial, so birds were required to search the entire screen and peck at the correct position during each trial. Once the birds had learned to do this, the difficulty of detecting the moth image was increased by introducing more cryptic backgrounds. Moths were presented on backgrounds of difficulty level one (10% of the pixel greyscale values were identical in frequency distribution to those of the moths, and 90% were from a uniform grey-scale distribution), which made the moths easily detectable, yet more difficult than finding the moths on an essentially empty background.

Next, a green circle in the center of the screen which accompanied moth images, the "giving up" key, was introduced. Birds were not rewarded for pecking at the green circle, but instead were immediately presented with a new start key screen. Next, birds were subjected to trials in which the green key was presented along with backgrounds containing no moth. In these trials, pecking the background at random caused the screen to go black, and the birds were forced to wait for 50 seconds before seeing the start key again. Pecking at the green circle, however, reduced the time between trials to 3 seconds. If the bird refused to peck at anything, the screen went black after 60 seconds, and the bird was forced to wait an additional 12 seconds between trials.

Training:

During training, each bird was presented with two moth types, each of which appeared in 25% of trials. The remaining 50% of trials were "negative" trials, in which there was no moth present, and the correct response was to peck at the green circle. After the bird successfully learned to peck at more than 90% of the moths when present, and the green circle on more than 90% of trials when moths were absent, backgrounds were adjusted (from level 1) so that moths became much more difficult to detect.

Backgrounds for each trial in the next stage were randomly selected from levels 1 through 4 inclusively. Detection rates were monitored daily, and when a bird exceeded

80% detection of the moths for both moth types for more than one consecutive day the overall background difficulty level was increased. That is, the range of levels from which a background might be selected for a given trial increased from 1-4 to 2-5, and so on. This titration process continued until the birds were responding to negatives correctly for more than 90% of negative trials and to the more difficult of the two positive stimuli for 70-80% of trials for four or more consecutive days. Actual background difficulty levels at the end of training were 3-6, for five of the birds. The sixth bird required backgrounds 4-7.

Testing:

Each day of testing, the birds were exposed to 70 positive and 70 negative trials. Within each 140 trial session there were three blocks of 32 test trials. In one block, the sixteen positive trials were a randomly ordered presentation of four moths of each type, along with an equal number of interspersed negative trials. This was the "non-run" condition. In the other blocks, the sixteen positive trials contained only a single moth type, interspersed with sixteen negative trials. These were the two "runs" conditions. The order in which the three block types were presented was balanced across days, and the starting points of the test blocks within the 140 trial session was shifted randomly each day. "Warmup" trials, and trials between test blocks were 50% negative, with the two moth types equally represented in the positive trials. For each trial, the trial type, background type, response of the bird, and reaction time were recorded for analysis.

Analysis:

To analyze stimulus sequence effects, accuracy and reaction time were calculated for each position in the sequence of trials for each treatment type. There were sixteen positive trials and sixteen negative trials for each treatment block each day. Positive trials were considered separately from negative trials, and each was blocked in groups of four.

Accuracy was calculated as the percent correct responses for each combination of bird, background difficulty, stimulus type, and position, separately for positive and negative trials. Reaction time was obtained by calculating the average response time for correct detection of a given moth type by a given bird under those treatment conditions.

RESULTS

General Searching Behavior:

The birds responded correctly more often when moths were absent than when they were present. Mean accuracy was 89.4 +/- 2.8% on negative trials and 75.0 +/- 3.7% on positive trials, $F(1,5) = 9.71$, $P < 0.05$. When birds responded correctly, they required less time to detect moths (6.1 s) than to peck the giving up key (16.9 s), $F(1,5) = 32.97$, $P < 0.01$. When the birds failed to detect moths, they usually pecked at the giving-up key. Birds pecked at the background outside the region containing the moth on just 2.6% of positive trials.

On positive trials, accuracy and reaction time were both influenced by background difficulty. Data from positive trials were analyzed with a background x moth by bird ANOVA. There were significant effects of background on accuracy, F(3,15) = 192.32, P < 0.001, and reaction time of correct responses, F(3,15) = 122.29, P < 0.001. Accuracy decreased (Figure 3C) and reaction time increased (Figure 3D) with increasing levels of background difficulty.

On negative trials, with no moth present, accuracy and reaction time followed similar trends. Accuracy decreased and reaction time increased with increasing background difficulty levels. However, a background by birds ANOVA found no effect of background on accuracy, F(3,15) < 1, or reaction time, F(3,15) < 1, on negative trials.

Sequence Effects on Positive Trials:

In order to demonstrate effects of inter-prey interval on runs effects, it was first necessary to demonstrate runs effects. Each daily session contained randomly ordered blocks of three different target-type treatments. There were treatments that included only type A moths, those that included only type B moths, and treatment blocks that were an equal and random mixture of the two moth types. Each of these treatment blocks was composed of 32 trials, 16 of which were positive trials that actually presented a moth image. Those 16 trials were broken up into four position blocks: positions 1-4, positions 5-8, positions 9-12, and positions 13-16.

To determine if there were changes in accuracy due to the presentation of single moth types, rather than mixed trials, the data were analyzed with a position x sequence type (run vs. non-run) x moth by bird ANOVA. The analysis revealed a significant main effect of position, F(3,15) = 6.82, $P < 0.01$, and a significant interaction of position x sequence-type treatment, F(3,15) = 10.42, $P < 0.05$. During runs treatment blocks, accuracy increased with experience at a greater rate than in the non-runs treatment (Figure 3E).

To test the hypothesis that reaction time decreased during runs treatments at a greater rate than when prey were presented in mixed sequences, a position x target type x background by bird ANOVA was utilized. There was no effect of position, F(3,15) < 1. Reaction time oscillated around 6.5 seconds, regardless of position or sequence type (Figure 3F).

Sequence Effects on Negative Trials:

To test the hypothesis that accuracy increased with experience during negative trials, the data for trials that did not contain moths were examined. A position x target type x background by bird ANOVA found a significant effect of position, F(2,10) = 7.10, $P < 0.05$, but there was no effect of target type, F(1,10) < 1, and no interaction of position and target type treatment, F(4,20) < 1. Accuracy on negative trials increased with experience regardless of target type (figure 3G).

To determine if reaction time on negative trials was influenced by target type, the data for trials that did not contain moths were subjected to a position x target type x background by bird ANOVA. There was no effect of position, F(2,10) < 1, and there was no effect of sequence type, F(2,10) < 1. There was virtually no change in reaction time across blocks on negative trials (Figure 3H).

Inter-prey Interval:

Probe trials were used to determine whether there were effects of inter-prey interval. Following the 9th positive trial in half of the runs blocks, delays of 0, 20, or 60 seconds were inserted to allow for potential decay of the searching image. Accuracy and reaction time for 84 replications of the 10th positive trial were then calculated for sessions in which there were 20 second delays, for sessions in which there were 60 second delays, and for those in which there was no delay. If the searching image strategy was interrupted by a delay, performance would be expected to decline in comparison to sessions in which there was no additional delay imposed.

To look for an effect of a delay on accuracy, data from the 10th positive trial of each of the runs blocks were analyzed with a moth x delay x background by bird ANOVA. Mean accuracy on the 10th positive trial of a runs block was 71.9% when there was no delay, and increased to 72.2% and 74.3% following 20 second and 60 second delays, respectively, (Figure 3I) but there was not a significant effect of delay, $F(2,10) < 1$. The birds were more accurate on moth A (82.3%) than moth B (66.6%), $F(1,5) = 7.56$, $P < 0.05$, but there was not a significant moth type x delay interaction, $F(1,2) < 1$ (Figure 3J).

To determine whether there were effects of delays on reaction time, data from the 10th positive trials of runs blocks were analyzed with a moth x delay x background by bird ANOVA. Reaction time for moth A (6.5 s) was faster than for moth B (9.2 s), $F(1,5) = 7.11$, $P < 0.05$. Average reaction time was 6.6 s following no delay, and increased to 9.1 s and 7.9 s following 20 second and 60 second delays, respectively, $F(1,10) = 5.45$. P <

0.05. (Figure 3K) A planned comparison found that reaction time on trials following a 20 second delay were significantly longer than following no delay, t=3.75, P = .004. N = 6. A planned comparison of reaction time following no delay and a delay of 60 seconds, found no effect of delay, t(5) = 1.70, P = 0.11.

In addition, there was a significant moth type x delay interaction, F(2,10) = 10.71, P < 0.01. Reaction time for moth B was greatest following a 20 second delay, but reaction time for moth A was greatest following a 60 second delay (Figure 3L). When data for detection of moth A was analyzed separately form moth B, in a delay x background by bird ANOVA, there was no effect of delay on reaction time, F(2,10) = 2.30, P = 0.15. When data for detection of moth B was considered alone, there was a significant effect of delay on reaction time, F(2,10) = 10.02, P < 0.01. However, planned comparisons revealed differences only between the no-delay and 20-second delay treatments. t(5) = 5.28, P = 0.001.

DISCUSSION

The results seem to provide little support for the memory decay model. While Plaisted found effects of delay on accuracy in pigeons, this study found no effects of inter-prey interval on accuracy. The only effect of inter-prey interval was found in reaction time data, and this was found for detection of only one of the two moth types following a 20 second delay. This may be interpreted as consistent with Plaisted's data, in that search efficiency was reduced following a delay. Because Plaisted's published data included only discrimination ratios, however, no direct comparison between the studies may be made for this measure. Furthermore, the presence of an effect following a 20 second delay and the absence of an effect following a 60 second delay seems counter to the memory decay hypothesis which suggests that performance should decrease with increasing delays. In addition, it seems that reaction time is generally more susceptible to variation and influenced less by previous searching experience than detection accuracy, as runs effects in this study were found only in accuracy data.

Effects of Inter-prey Interval:

To test the hypothesis that runs effects can be disrupted due to memory decay, delays of 0, 20, or 60 seconds were inserted following the ninth positive trial of runs treatment blocks. If removing moths from sight for a period of time results in a decrease in detection accuracy, it would provide support for the memory-decay model. In this experiment, however, accuracy in positive trials immediately following such delays did not decline. Furthermore, mean accuracy following 20 and 60 second delays were slightly higher than when there was no delay. Thus it seems unlikely that the delays negatively influenced the ability of the predator to retain a searching image.

More perplexing is the finding that reaction time, in trials in which the birds correctly detected moths in the 10th positive trial, were influenced by delays. Reaction time increased from 6.6 seconds under control conditions to 9.1 seconds following a 20 second delay and 7.9 seconds following a 60 second delay. Only the reaction time differences between no-delay and 20-second delay treatments were significant.

Consequently, it appears that there were effects of delay on this measure of detection performance, but the nature of these effects remains unclear.

The results do not seem to be consistent with the memory decay hypothesis. Not only was the reaction time longest following a 20-second delay, rather than following a 60-second delay, but there was a significant moth by delay interaction. The birds needed more time to find moth B after a delay of 20 seconds than after a delay of 60 seconds, and they needed more time to find moth A after a delay of 60 seconds than after a delay of 20 seconds, although only the former difference was statistically significant. Perhaps any consideration of these effects should be done with caution. The reaction time data is not normally distributed, and the averages may have been skewed by a small number of trials with exceptionally long reaction times.

Runs Effects:

Birds were exposed to moths in sequences that included runs of a single moth type (with positive and negative trials intermixed) or sequences that were presentations of two different moth types in random order. If a bird utilizes a searching image for a moth when exposed to a runs sequence, the bird's performance may increase as it progresses through the block. Presentation of two moth types in random order should not promote the use of a searching image, as a bird utilizing a searching image for one moth type would be more likely to overlook the other target type. Consequently, under non-runs conditions, performance is expected to be relatively stable, as the birds settle for a more general strategy to find whichever moth is present.

There are multiple measurements of performance used in searching images studies. One of them, reaction time for positive trials, is expected to decrease during runs blocks in comparison to non-runs blocks. The results of this experiment, however, provided no support for this prediction, as reaction time seemed to oscillate between 6 and 6.5 seconds across position blocks, regardless of presentation sequence. It seems that runs effects are more difficult to demonstrate using reaction time data. For example, Bond & Kamil (1999) found highly significant effects on accuracy, but no effect on response time. Variability in the data may be a consequence of the use of a touch screen; while it ensures that a moth located a cryptic target, a bird may have to move across the perch in order to reach the position of a moth.

There were effects in this experiment of sequence type on accuracy. During runs, average accuracy increased from 70% to 75%, while accuracy during non-runs increased only 2%. While the effect of position and the interaction of position and sequence type were significant, the effect is not particularly strong, especially in comparison to results found by Pietrewicz and Kamil (1979) which reported increases of nearly 20% during runs, and a slight decrease in accuracy during non-runs. The reasons for these differences are likely to be two-fold. First, one of the moths in this study was relatively conspicuous. Because this target type was easy to detect regardless of previous experience, there was little room for improvement in detection of this moth type during runs. Increases in accuracy during runs treatments likely would have been more dramatic had both moths been sufficiently cryptic. The second reason for differences between this study and those by Pietrewicz and Kamil (1979) may be the use of multiple sequence type blocks within a single session. Although there were buffer trials between test blocks, these may not have separated treatments to the same degree as returning the birds to their home cages, as was done in the earlier study. The possibility of carry-over effects from runs blocks to non-runs blocks cannot be ruled out.

General Searching:

The general searching behavior of the birds in this experiment was similar to that shown in previous experiments of this type. Birds were more accurate on negative trials than they were when moths were present. This is likely the result of the high cost of false positives (Bond & Kamil, 1999; Bond & Riley, 1991). That is, to avoid the punishment of a 30 second delay before the next trial, birds rarely pecked at the background unless a moth had been detected.

While aversion to long inter-trial intervals may have influenced accuracy, reaction time was influenced by the potential for reward. To avoid missed opportunities for food reward, the birds rarely pecked at the "move on" key as quickly as they pecked at detected moths. The data is consistent with an exhaustive search, in which the birds scanned the entire background at least once before choosing to advance to the next trial (Sternberg, 1975; Triesman & Gelade, 1980).

Implications:

While these results are generally in agreement with those of Bond & Kamil (1999) and appear to be in conflict with those of Plaisted (1997), many issues remain. It is still unclear whether these differences are the result of differences in presentation, in the stimuli, or in the subjects. For example, Plaisted's apparatus utilized a response key to be pecked by the birds when a target was present; because the birds were not required to peck at the location in which the target appeared, and because the punishment for incorrect pecks was less severe, the birds may have been more inclined to peck regardless of actual stimulus detection, perhaps based on elapsed time. In addition, Bond & Kamil (1999) noted that there might be differences due to rather conspicuous target types used by Plaisted. This seems an unlikely explanation for some of her results, however, as Figure 3 (Plaisted, 1997) appears to provide a clear demonstration that under certain conditions, the accuracy of the pigeons across trial blocks remained relatively low. Bond & Kamil (1999) also noted that number of targets might be a factor, given that Plaisted used only two and that Vreven and Blough (1998) have shown that experienced pigeons can search for sets of six targets simultaneously. Despite these problems, it may be that none of these explanations are completely satisfying because some of the most important differences in the results may be related to species differences. If pigeons primarily feed upon seeds spread across the ground (Murton & Westwood, 1966) and blue jays frequently search for cryptic insects such as *Catocala* moths resting on the bark of trees (Sargent, 1976), then it seems likely that there is stronger selection for blue jays to retain a searching image for longer durations.

Given the likelihood of differences in cognitive abilities between predator species, further study of the effects of inter-prey interval seem warranted. Perhaps blue jays should be subjected to longer delays between presentations of the same target type.

A complication in the design of such experiments, however, is the use of the punishment and reward contingencies that have so often been used. In this experiment, and in those that inspired it, birds were required to make a choice between attacking a moth, if they found one, and leaving the patch. If a bird attacked a piece of "bark" that resembled a food item, it was punished with a time delay which simulated what a bird in the woods might have experienced under those circumstances; the bird either spent too much time in an unproductive patch, or it gave a nearby moth an opportunity to escape. The birds are quite responsive to these time delays and seem to avoid them at all costs. This responsiveness creates experimental design difficulties. The problem lies in presenting additional delays as experimental treatments without disrupting the birds. A pilot study that preceded this experiment found that when 60 second delays were inserted between each of 16 trials in a block, the birds simply aborted the sessions by refusing to respond to additional stimuli presented (to even start a new trial).

Consequently, further studies might involve a comparison of pigeons and blue jays in a delayed matching to sample task, similar to that used by Wilson and Boakes (1985) to compare short term memory in pigeons and jackdaws. Alternatively, studies might continue along the prey detection line, but follow the example of Bond & Kamil (1999) in utilization of the time between correct detections as a measure of inter-prey interval. As long as the birds are looking for moths on backgrounds that do not contain moths, or as long as they are overlooking moths that are present, the birds will remain motivated to continue sessions without being encouraged to make false positives.

Conclusions:

The results of the experiment suggest that experience with prey induces short-term changes in the ability of blue jays to detect cryptic prey. When the prey-detection process was interrupted by an inter-trial interval of 20 seconds or 60 seconds, the birds showed no decline in accuracy in the next trial containing a moth image. This seems to suggest that Plaisted's (1997) results, which suggested that searching images decayed after 20 second delays in pigeons, do not necessarily apply to blue jays. Because it is unlikely that blue jays in nature encounter cryptic prey more frequently than every 20 seconds, this demonstration is important. However, because the effects do not last indefinitely, additional studies are necessary to determine how long they last without reinforcement. In addition, it would be interesting to determine whether prey distribute themselves in space (and bird time) to reduce predator success. If prey can assess local morph frequency and move if the density is high, they may reduce the likelihood of being discovered by a predator utilizing the appropriate searching image. However, there may be a trade-off if suitable backgrounds are clumped.

CHAPTER 4: PREY SYMMETRY AND DETECTION

INTRODUCTION

Early studies of searching images showed that birds were better able to detect cryptic prey when they encountered them repeatedly (Tinbergen, 1960; Croze 1970). Subsequent studies tested the hypothesis under more controlled conditions to show more clearly that the effect is the result of changes in visual perception rather than the result of a preference for a more palatable prey type or for a prey type that is easier to handle (Dawkins, 1971; Gendron, 1986). Additional studies demonstrated that changes in performance can be shown to be independent of the rate with which a bird searches for cryptic prey (Pietrewicz, 1979; Reid & Shettleworth, 1992), and studies have even shown that predators utilizing searching images can maintain polymorphism in prey populations through apostatic selection (Bond & Kamil, 1998).

Because the use of searching images may play an important role in ecology and the evolution of prey species, there is interest in understanding additional details about the use of searching images. Some factors are thought to be likely to enhance searching image effects, while others make utilization of searching images ineffective. For example, Kono et al.(1998) investigated whether searching image effects could be enhanced by predator use of environmental cues through priming, and others have questioned whether birds might have a more difficult time if there are long periods of time in which the bird does not encounter prey (Plaisted, 1997; Bond & Kamil, 1999).

While factors such as priming by environmental cues and inter-prey interval are potentially important influences on performance after a bird has acquired a searching image, little is known about the factors that influence how the searching image is initially acquired. The original field studies suggested that a searching image is likely to be formed for prey that are relatively common (Tinbergen, 1960), so raw numbers may be important. Crypticity also plays a role, since strong searching image effects seem to result when stimuli are quite difficult to detect (Blough, 1989; Bond & Kamil,1999). Thus it seems that prey must be cryptic, but they must also be so common that they may be occasionally discovered. For example, while moths rarely move during the day, the likelihood of seeing such movement increases with moth density. In addition, some insect prey types may cause leaf damage, to which birds may be sensitive (Real et al., 1984), and such damage increases with large prey numbers. Similarly, increasing numbers of cryptic prey may increase the likelihood of being seen by selecting the wrong background. Operant studies of searching images generally seem to make the assumption that prey items sometimes select the wrong substrate, as birds are frequently trained to peck at stimuli before the crypticity is increased through background manipulation. There is a possibility, however, that birds utilize other cues about the appearance of prey to help them find cryptic prey without the aid of searching image.

Symmetry might provide a cue that birds use to find cryptic prey. Curio (1976) hypothesized that the concept of bilateral symmetry might aid birds in recognizing camouflaged prey, and a number of bird species have been shown to be able to detect and respond to symmetric visual stimuli (Delius and Nowak,1982; Blough & Franklin, 1985;

Moller, 1993; Swaddle & Cuthill 1994, Fiske & Amundsen, 1997). Although discriminating between stimuli based on symmetry and finding cryptic symmetric prey are quite different tasks, Julesz (1969) found that human subjects readily notice symmetry in random dot patterns.

Once a symmetric target has been identified, the symmetry of a prey item may influence the ability of the bird to create a mental representation of the visual appearance of the prey. Locher & Nodine (1973) argue that since the features of one half of the shape are redundant with those of the other half, subjects need only attend to half of the image. And, since the informational context is decreased by the similarities (Michels and Zusne, 1965) the searching image may be more efficiently utilized.

If symmetry really is an important cue, one might expect to find many examples of cryptic prey that deviate from symmetry. A survey of organisms, however reveals otherwise. For some animals, symmetry is very important. Birds with symmetrical flight feathers, for example, achieve more efficient flight (Swaddle et al, 1996; Moller 1991), and consequently, they are better able to obtain food and escape prey (Moller, 1992; Moller & Nielsen, 1997). Thus, it appears that there are serious consequences of asymmetrical body shapes, and there is evidence that animals look for symmetry when choosing mates (Moller, 1993; Arcese, 1994). On the other hand, body shape should not be confused with body pattern. There are certainly examples of frogs and salamanders with asymmetrical spot patterns (Neville, 1976), and these patterns have no discernable effect on the ability to move about.

Moths with symmetrical wing shapes and asymmetrical wing patterns may be able to move about as well as any other moths. Furthermore, wing pattern seems less likely to play an important role in mate attraction in a species like *Catocala,* which attracts mates through pheromones (Sargent, 1976). In such a species, then, it seems that wing pattern symmetry has high costs and low benefits, yet symmetry remains the norm.

To find an explanation for this evolutionary puzzle, prey items need to be examined in greater detail. The developmental constraints and linkages between various traits in the organisms need to be better understood. Equally important, however, is a demonstration that these costs of symmetry are real. A clear demonstration that symmetrical moths are more conspicuous and more amenable to the use of searching image by their predators would give substance to the theoretical arguments.

To address this issue, both symmetric and asymmetric digitized moth images were presented to blue jays in an operant setup. Birds were provided with food rewards for pecking at moth images which were overlaid upon complex artificial backgrounds which rendered them cryptic to human eyes. It was expected that moth symmetry would be a salient cue, given that there were no intentional symmetric patterns in the backgrounds. It was also expected that symmetric patterns would be easier to remember, resulting in higher performance on symmetric moths than asymmetric moths when presented frequently within a single session.

EXPERIMENT 4.1: DETECTION OF SYMMETRIC AND ASYMMETRIC PREY

Experiment 4.1 compared the ability of blue jays to detect six bilaterally symmetric moths to the ability to detect six asymmetric moths, created by randomly combining left and right halves of the six symmetric moth images. The birds were exposed to each of the 12 moths 3 times per day in random order, intermixed with 36 trials containing only backgrounds.

METHODS

Subjects:

Six blue jays (*Cyanocitta cristata*), collected as fledglings and reared in the lab, from 2 to 3 years of age, were used as predators. All birds were experimentally naive and had never searched for either symmetric or asymmetric stimuli. All were maintained at 80-85% of their free-feeding weight in individual cages on a 14:10 light:dark cycle. and training and experimental trials were conducted between 7 am and 4 pm.

Backgrounds:

Backgrounds were created by an algorithm that selected a greyscale value at random for each pixel in the rectangular field. To create varying levels of crypticity, backgrounds were created by combining different percentages of pixels from the combined moth image frequency distribution from the moths in a previous experiment and from a uniform grey-scale distribution. A background of level two was created from 20% of the moth pool, level three from 30%, and so on. Manipulating the proportion of background pixels selected from each distribution indirectly controlled the difficulty with which the birds were able to detect moth images. In order to quickly present new backgrounds for each session, new backgrounds were generated and saved as large graphics files between testing sessions.

Stimuli:

Moth images for this study were created with the algorithm that was used to create a background image of difficulty level six. For each symmetrical moth, a block of pixels (8 wide x 16 high) was generated using the background generating algorithm. From this block, pixels were removed (actually made transparent) from the upper left corner and lower right corner in order to produce a shape resembling a moth wing. Next a mirror image was created to form a right half of the previously generated left half. These two shapes were combined to form a moth-like image, and the process was repeated six times to form the six symmetrical moths seen by the birds.

For each bird, six asymmetrical images were also created. The left half of each of the symmetrical moths was combined with the right half a different symmetrical moth. For example, one of the moths presented to bird 141 was created by combining moth A and moth F, and one of the moths presented to bird 142 was created by combining moth F and moth D. In this manner, every conceivable combination of left and right half-moth was used as a stimulus (Figure 4A).

Apparatus:

The birds were tested in a 52 cm high x 36 cm wide x 62 cm long galvanized steel operant box. A touch screen, which detected the location of pecks at stimuli was located within the operant chamber and within 2 cm of the face of the monitor. A piece of plexiglass mounted on foam pads near the screen of the monitor reduced the impacts of the pecks on the beaks of the birds. A speaker for a white noise generator was positioned on one side, to reduce distractions from outside noise, and an overhead light was positioned above the monitor to illuminate the perch. A perch was positioned so that it was at the same height as the bottom of the monitor screen and 12 cm from the plexiglass. An opening in the floor of the operant box, beneath the perch, allowed the birds to reach and retrieve food rewards. These food rewards were delivered by a lazy suzan style feeder.

Procedure-

Pretraining:

After habituation to the operant box and magazine training, in which food rewards were provided at random time intervals, blue jays were hand-shaped to peck at the computer monitor by learning to associate pecking at conspicuous moth stimuli in a fixed position on the computer screen with a food reward. The symmetric and asymmetric moth images were the same size and shape as those used during testing, but for training purposes were presented on a neutral gray background so that they were quite easy to see.

Initially, food rewards were provided when birds merely looked at these stimuli, and were later only provided when the birds pecked at the images.

After the birds learned to peck at moth images for food rewards, they were trained to peck at a red circle in the middle of the monitor screen. This peck at the 'start key' started the next phase of the trial: The red circle disappeared and was replaced by the image of the moth. When the bird pecked within 2 cm of the center of this moth image, a food reward was delivered. The start key procedure was used to allow the bird to start each trial, which reduced the variability of latency measures.

In the next stage, the location of the moth images on the screen varied at random from trial to trial, so birds were required to search the entire screen and peck at the correct position during each trial. Once the birds had learned to do this, the difficulty of detecting the moth image was increased by introducing more cryptic backgrounds. Moths were initially presented on backgrounds of difficulty level one (10% of the pixel greyscale values were identical in frequency distribution to those of the moths, and 90% were from a uniform grey-scale distribution), which made the moths easily detectable, yet more difficult than finding the moths on an essentially empty background.

Next, the 'giving up' key, a green circle in the center of the screen which accompanied moth images, was introduced. Birds were not rewarded for pecking at the green circle, but instead were immediately presented with a new start key screen. Next, birds were subjected to trials in which the green key was presented along with backgrounds containing no moth. In these trials, pecking the background at random caused the screen to go black, and the birds were forced to wait for 50 seconds before seeing the start key again. Pecking at the green circle, however, reduced the time between trials to 3 seconds. If the bird refused to peck at anything, the screen went black after 60 seconds, and the bird was forced to wait an additional 12 seconds between trials.

Training:

After the bird successfully learned to peck at more than 90% of the moths when present, and at the green circle on more than 90% of trials when moths were absent, backgrounds were adjusted so that moths became much more difficult to detect. During training, each bird was presented with the each of 12 moths three times per day. An additional 36 trials were "negative" trials, in which there was no moth present, and the correct response was to peck at the green circle.

When the birds were responding to negatives correctly for more than 90% of trials and to the positive stimuli for 70-80% of trials for four or more consecutive days, the testing phase began. To achieve this, detection rates were monitored daily during training. When birds exceeded 80% detection for two successive days, the background difficulty was increased. When performance fell below 70% detection for two or more days, the background difficulty level was reduced.

Testing:

Each day of 20 days of testing, the birds were exposed to 36 positive and 36 negative trials. The 36 positive trials included 3 presentations for each of 12 moths. Six of the 12 moths were symmetrical, and six were asymmetrical. In addition, background difficulty level (one of two) was selected at random for each trial. For each trial, the trial type, background difficulty, moth type, response, and reaction time of the bird were recorded for analysis.

Analysis:

For each bird, mean accuracy was calculated for the six symmetric moths and six asymmetric moths. Accuracy and reaction time for symmetric and asymmetric moths were compared using repeated measures analyses of variance.

RESULTS AND DISCUSSION

During test sessions, mean accuracy was 81.8% for symmetric moths and 79.7% for asymmetric moths (Figure 4B). A symmetry x background by bird ANOVA found a significant effect of background, F(1,5) = 153.09, $P < 0.001$, but there was no effect of symmetry on accuracy, F(1,5) = 3.30. Although it appeared that there were greater differences in accuracy due to symmetry for background level 3 than for level 2, there was no symmetry x backgound interaction F(1,5) = 1.70.

Mean reaction time for correct moth detections was 3.8 s for symmetric moths and 4.0 s for asymmetric moths (Figure 4C). A symmetry x background by bird ANOVA found a significant effect of background, F(1,5) = 12.50, $P < 0.05$, but there was no effect of symmetry on reaction time, F(1,5) = 1.06. Although it appeared that there were greater differences in reaction time due to symmetry for background level 3 than for level 2, there was no symmetry x background interaction F(1,5) = 1.70.

While the overall results provide no statistical support for the hypothesis that birds can use symmetry as a cue for detection of cryptic prey, overall accuracy was high. It appeared that there were greater differences between the symmetric and asymmetric means when the moths were found on background level 3, suggesting that greater background difficulty levels might be necessary to elicit effects.

EXPERIMENT 4.2: DETECTION COMPARISONS WITH HIGHER CRYPTICITY

One interpretation of the results of experiment 4.1 is that, the background level used was insufficient to provide protection to any of the moths. Had the backgrounds been more similar to the moths been used, symmetric moths would have been more consistently detected than asymmetric moths. Adjusting the background difficulty levels seemed to be a necessary step towards such a demonstration.

A search for effects of symmetry could be complicated, however, by the expectations of the birds. If a bird were able to find only a small percentage of the moths on the screen during a session, it might be inclined to peck indiscriminately at the background, despite the punishment of a long inter-trial interval. Alternatively it might not find the effort of searching and pecking to be worthwhile, given that it would receive daily food rations in its homecage, regardless of performance in the operant box. To counter these potential problems, the birds were presented with each moth three times per day, each time on a different background. Each moth appeared on backgrounds of level 1, where it was conspicuous, and virtually guaranteed detection success. Each moth also appeared on a level 3 background and a level 5 background. Detection performance on level 5 backgrounds was the primary measure of interest.

METHODS

All subjects, stimuli, and apparatus were identical to those described in experiment 4.1. Background difficulty levels were increased for one third of trials and decreased for one third of trials.

RESULTS AND DISCUSSION

During test sessions, accuracy was slightly lower, and reaction times were slightly longer than in experiment 4.1. Mean accuracy across all background levels was 69.9% for symmetric moths and 66.9% for asymmetric moths (Figure 4D). Detection performance decreased with increasing background difficulty levels, $F(2,5) = 153.09$, $P < 0.001$. Symmetric moths were detected more often than asymmetric moths across all backgrounds, but the difference was not statistically significant, $F(1,5) = 5.59$, $P = .064$. Mean reaction time for correct moth detections was 5.2 s for symmetric moths and 4.9 s for asymmetric moths (Figure 4E). A symmetry x background by bird ANOVA found a significant effect of background, $F(2,5) = 24.51$, $P < 0.001$, but there was no effect of symmetry on reaction time, $F(1,5) < 1$.

While the effect of symmetry on accuracy was not significant overall, any effect was expected to be strongest under conditions created by background level 5, where patterns were most similar to those on the wings of the moths. Data from positive trials on background level 5 were therefore extracted and subjected to a paired sample t-test.

Symmetrical moths were detected significantly more often than asymmetric moths. t(5) = 3.84, P = .012.

While mean accuracy on symmetric and asymmetric moths (27.5% and 19.8%, respectively) suggested that the detection task was difficult at this level, task difficulty could also be estimated by accuracy on negative trials. A background x bird ANOVA found a highly significant effect of background on accuracy during negative trials, F(2,5) = 37.59, P < .01. While accuracy was over 95% when backgrounds of level 1 were presented, accuracy when backgrounds of level 5 were presented was less than 60% (Figure 4F). Birds frequently pecked indiscriminately at the background when faced with such difficult detection tasks.

EXPERIMENT 4.3: A VIRTUAL PREY APPROACH TO SYMMETRY QUESTIONS

The results of the first two experiments suggested that at some background difficulty levels, symmetric moths were easier to detect than asymmetric moths. How this might apply to the natural environment was somewhat unclear. If a bird feeding primarily upon symmetrical morphs encountered an asymmetrical moth, would the prey be recognized? Might such a prey type be overlooked so frequently that it could increase in numbers while symmetrical morphs declined as a result of predation? To address these questions, the “virtual prey” technique (Bond and Kamil, 1998) was utilized. A population of 3 symmetrical moth types was generated, and six experienced birds were given daily hunting opportunities. Prey populations were regenerated on a daily basis in response to the predation rates on each of these moth types. After 30 generations, two new moths types were introduced into the populations. One type was symmetric, the other asymmetric. Rates of population increase for the two types were compared to determine whether there were effects of symmetry.

METHODS

Subjects:

Six blue jays (*Cyanocitta cristata*), collected as fledglings and reared in the lab, from 6 to 18 years of age, were used as predators. All birds had previous operant experience searching for symmetric cryptic moths. All were maintained at 80-85% of their free-feeding weight in individual cages on a 14:10 light:dark cycle, and training and experimental trials were conducted between 7 am and 4 pm.

Backgrounds & Stimuli:

Background and moth stimuli were generated using the same techniques as in experiments 4.1 and 4.2. The three symmetric moths of the original population were actually identical to three of the symmetrical moths used in experiments 4.1 and 4.2. The birds in that experiment found these three to be most similar in crypticity. Each of the novel moths was unique to this experiment. Distinctive patterns were generated to produce both left and right halves of asymmetrical moths, and entirely different patterns were used to create the symmetrical moths (Figure 4G).

Procedure:

Pretraining & Training:

Birds were trained using the same methods as in experiment 4.1, except that three symmetrical moth types were presented to the birds. The moth images were presented on backgrounds that made them appear conspicuous for two weeks before the virtual population was ready.

Testing:

In each session, five levels of background difficulty were used, ranging from 2 to 6. Birds were exposed to 120 trials, 36 of which were positives. If a bird pecked at a moth, it received a food reward. If it did not find a moth, it could peck at the "move on" key to advance to the next trial. When a bird pecked at a moth, it was considered "killed" and was removed from the population. When all six birds had completed a given session, the population was regenerated, based on the relative abundance of the surviving prey. For example, while there might initially be 33.3% of each of three moth types in the population, one moth type might be more easily detected than the other two. Consequently, at the end of the day, the proportion of the conspicuous type in the surviving population would be lower than the others. The population would then be regenerated to produce a population of the same size as at beginning of the previous day, but the proportion of the conspicuous moth type would be much lower (and equal to the proportion at the end of the previous day).

Each replication of the experiment began with a founding population consisting of equal numbers of symmetric moths 1, 2, & 3. After 30 generations, two additional moth types were introduced. each initially making up 3% of the total population. One was bilaterally symmetrical, and the other was highly asymmetrical. The birds were allowed to continue to peck at moths and influence the abundance of prey types for an additional 14 generations, after which the population was returned to baseline for a new replication.

RESULTS AND DISCUSSION

In the first replication, it appeared that the birds found the new asymmetric moth to be quite cryptic. It increased in frequency, while the familiar symmetrical moths 1 and 3, from the original population, decreased in numbers. The new symmetrical moth. in contrast, never climbed above 4% (Figure 4H).

In the second replication, the results were less striking; the frequency of both moth types increased at approximately the same rates (Figure 4I). In the third replication, the symmetric moth increased in numbers at a much faster rate, suggesting the birds found the asymmetric moth to be more conspicuous. Thus, each of the three possible outcomes were expressed in the first three replications of the experiment.

In the fourth replication, asymmetric moths increased at a greater rate. In the fifth replication, symmetric and asymmetric moths increased at nearly the same rate. In the sixth replication, symmetric and asymmetric moths increased at the same rate for the first

7 generations, but asymmetric moths were ultimately more cryptic. In the seventh replication, asymmetric moths increased in numbers at a greater rate than symmetric moths. Asymmetric moths clearly increased at greater rates than symmetric moths in 4 of 7 replications (Figure 4I).

Slopes of the changes in population number for the introduced moth types were calculated and compared using a paired sample t-test. There was no significant effect of symmetry on population growth, $t(6) = .47$, $P = 0.65$. This result suggests that symmetrical moths are not necessarily at a disadvantage. While birds sometimes overlooked some new asymmetrical moths, other asymmetrical moths were apparently quite conspicuous. Consequently, it appears that effective background matching is possible, even when a prey item is highly symmetrical.

GENERAL DISCUSSION

The purpose of this study was to examine the influence of prey symmetry on detection, to determine whether birds utilize this cue prior to formation of a searching image and to determine whether a symmetrical prey type was more likely to be incorporated into a searching image. The results suggest that symmetry may not be a particularly important factor. Symmetrical moths can be quite cryptic, and asymmetrical moths can be conspicuous.

In experiments 4.1 and 4.2, birds were tested in their ability to detect 6 symmetric and 6 asymmetric moths. When the backgrounds used did not closely resemble the patterns of the moths, as in experiment 4.1, there was no effect of symmetry on detection.

When backgrounds were a close match, there was a significant effect of symmetry on detection. However, the results are not in complete agreement with the hypothesis that birds search on the basis of symmetry under such conditions. Had the birds actually been searching for symmetrical patterns on the background, it seems unlikely that the birds would have pecked so frequently at empty backgrounds.

The results, however, may be related to the special training conditions. For example, symmetrical and asymmetrical moths were presented to the naive birds in equal numbers. In addition, the two types of moths were initially presented to the birds under conditions that made them completely conspicuous. As a consequence the birds may have learned what to look for, and they may have been able to learn to detect all 12 moths, regardless of symmetry, even when conditions changed and the moths became more cryptic. That is, with considerable training experience, birds may form searching images for asymmetric moths.

Training effects do not, however, explain the frequent detection of novel asymmetrical moths in experiment 4.3. In experiment 4.3, a group of experienced birds preyed upon a virtual population of moths. After 30 days of searching for 3 symmetrical moth types, 2 additional morphs were introduced in small numbers into the population. The new symmetric morph was expected to be easier to detect and incorporate into a new searching image, but in several replications, the symmetric moth was more cryptic and more often overlooked. Perhaps more perplexing is that given much experience with symmetrical moths, both in this experiment and in previous studies, the birds used in experiment 4.3 apparently ignored this factor. They often failed to detect new symmetrical moths.

The results of the experiments are surprising in light of the extensive literature on bilateral symmetry detection in humans (Fitts, 1956, Attneave, 1967; Corballis & Roldan, 1974; Bornstein & Stiles-Davis, 1984; Biederman, 1987; Leyton, 1992) . On the other hand, the experiments were unique in that the stimuli were presented on backgrounds intended to produce crypticity. Like humans, blue jays may be quite capable of discriminating between symmetric and asymmetric objects, but the birds may not look for symmetry when looking for prey.

Under limited circumstances, symmetry may influence prey detection. There were significant difference in mean crypticity between symmetric and asymmetric moths on a background of level 5. However, nearly three-quarters of the symmetric moths presented to the birds in that treatment were overlooked. Consequently, while there may not be a heritable basis for asymmetric patterns in moths (Brakefield & Breuker, 1996; Windig, 1997), it may also be unnecessary.

CHAPTER 5: SUMMARY AND CONCLUSIONS

Birds that repeatedly encounter the same cryptic prey type can increase their searching efficiency through the use of a searching image, a sort of mental template of the visual features of the prey. A potential result of such a strategy is apostatic selection, which can ultimately produce polymorphic populations. Consequently, over the past four decades, there has been considerable interest in the interaction between the cognitive processes of avian predators and the appearance of their insect prey (Tinbergen 1960, Allen & Clarke, 1968; Dawkins, 1971; Pietrewicz & Kamil, 1979; Fullick & Greenwood 1979; Gendron 1986, Guilford & Dawkins, 1987; Bond & Riley, 1991; Reid & Shettleworth, 1992; Bond & Kamil, 1999). Over time, the experimental techniques for exploring this relationship have changed to provide researchers with increasing levels of control. While early studies were able to demonstrate that birds tended to take prey in runs of a single prey type (Tinbergen, 1960; Croze, 1970), recent studies have been able to control the sequence with which birds actually encounter prey, to show how performance is enhanced by repeated encounters of the same prey type, relative to encounters with two or more prey types encountered in random order (Pietrewicz & Kamil, 1979; Bond & Kamil, 1999).

My first objective was to take what seemed to be the next logical step, to control not only the sequence of such encounters, but to begin to manipulate the appearance of prey types. Through such investigations, it seemed possible to better understand the degree to which searching images reduce the likelihood of detection of alternative phenotypes and to elucidate what constitutes a true alternative phenotype. In addition, it seemed important to manipulate inter-prey interval, to understand how long searching images last and why they might be lost. Finally, it seemed reasonable to question whether some traits make even cryptic prey sufficiently detectable to promote the acquisition of a searching image for some prey types.

Through the use of operant techniques and sophisticated computer software and hardware, I was largely successful in my attempts to address these issues. I found in chapter 2 that I could manipulate the appearance of a prototype moth image to create a second phenotype, and I could show that birds responded differently to moth pairs depending upon the degree of similarity in the appearance of the two moth types. For example, when birds were presented a prototype moth and a moth that was considerably different from the prototype, birds showed no improvement in detection performance when the moths were presented in a random sequence. When either of the moths was presented in a sequence containing only that moth type, however, accuracy improved with experience, suggesting that a searching image was utilized only when moths were presented in runs sequences.

When the birds were presented with a prototype and a manipulated moth that were fairly similar in appearance, performance improved regardless of presentation sequence. Even when the two moths were presented in random order, experience in detection of one moth type apparently aided in the ability to find moths of the other type. This suggests that birds can generalize searching images to some extent, allowing them to find moths that differ slightly from others that they have recently detected.

However, when birds were presented with manipulated moths that differed most drastically from the prototype moths, the birds found them, regardless of presentation sequence. This suggests that because the patterns on the wings of moths are uniquely adapted to the backgrounds they rest upon, mutations may cause changes that reduce crypticity. Consequently, even a bird utilizing a searching image for the cryptic prototype moth is unlikely to overlook a drastically manipulated mutant.

While the results of the manipulated polymorphism study demonstrate the flexibility of the operant technique, they also illustrate that even under highly controlled conditions, predation pressure on the appearance of prey is complex. Morphs that are different from others in the population may escape the searching image of a predator, but morphs that are different from others in the population may lack features that enable them to blend into the background, thus increasing the likelihood of detection.

In chapter 3, I addressed the issue of inter-prey intervals. While repeated presentations of a single moth type facilitate the ability of birds to form searching images, and random sequences of two or more moth types appear to interfere with searching image formation, it has been argued that non-runs treatments actually demonstrate memory decay. When prey are presented at random, time spent during trials containing moth B may allow memory of the appearance of moth A to decay. The results of chapter 3 do not seem to support this memory decay hypothesis. When time delays of 0, 20, or 60 seconds were inserted between the 9th and 10th positive trials during runs treatments, there were no effects of delay on accuracy. There was a significant effect of delay on reaction time for the more cryptic moth type following a 20 second delay. However, because there was no such effect following a delay of 60 seconds, the memory decay hypothesis does not seem to be well supported, at least over the time intervals tested.

In chapter 4, I attempted to address the issue of the effects of prey symmetry on crypticity. Using background difficulty levels that have been shown to be sufficient for demonstrations of runs effects, I presented 6 symmetric moths and 6 asymmetric moths to blue jays. There was no effect of symmetry on the ability of the birds to detect the moths. When background difficulty levels were increased considerably, birds were able to find more of the symmetric moths than the asymmetric moths. However, under such conditions, birds also frequently pecked at empty backgrounds. Because such pecks were costly, in that they resulted in additional delays between trials, birds were not expected to peck at the background if they did not actually detect a moth. Consequently, some of the correct responses during positive trials may also have resulted from "guesses." In my final experiment, I attempted to determine if, as Curio (1976) suggested, asymmetric prey are more conspicuous than asymmetric prey, and consequently more likely to be overlooked by hunting jays. Over seven replications, the average increase in population numbers over 14 generations was no greater for novel symmetric moths than for novel asymmetric moths. Consequently, it does not appear likely that birds use symmetry as a cue to locate cryptic prey prior to the use of a searching image. Furthermore, it does not appear that birds have greater difficulty acquiring or deploying a searching image for an asymmetric target.

While the results of these experiments add to our general understanding of the use of searching images, and to the factors that do (or do not) influence searching image use, a number of additional questions have been raised. For example, it seems that birds do not look for symmetrical patterns when faced with the dilemma of finding a novel prey type. Consequently, they are no more likely to form searching images for symmetric prey items than asymmetric prey items, and the issues of symmetry and searching images appear not to be directly related. Still, the issue is intriguing: Are birds less sensitive to symmetry than humans, or is correct background matching by pattern and color sufficient to conceal this property? The next step in the search for this answer is to repeat the symmetry detection experiment using other animals as subjects.

More puzzling, and directly relevant to the topic of searching images, is the transition from the use of searching images as circumstances change and become less favorable for their use. The results of chapter 3 suggest that birds that face a blank screen for 20 or 60 seconds during the course of a runs block show no reduction in detection accuracy on the following positive trial. It isn't clear whether there is some sort of rehearsal involved (repeating of information in memory), but it appears that the image remains activated in memory for some time.

In chapter 2, during non-runs blocks that followed runs blocks, accuracy following 2 or fewer prior detections was low. This suggests that birds continued to search for the moth type that they had repeatedly encountered in the previous runs block. By the end of the non-runs block (following 3 or more prior detections), however, performance had improved considerably, suggesting that the birds had adjusted their strategy to find both moth types. In fact, performance at the end of non-runs blocks that followed one or more runs block in a daily session was higher than at the end of non-runs blocks that were the first treatment block of a session. This suggests that the searching image utilized earlier in the session may have increased performance during non-runs by allowing the bird to acquire and use a second searching image in parallel with the first.

To more effectively evaluate this hypothesis, however, much more data is necessary than was available from the design of the experiment in chapter 2. Each moth type should be presented at least 8 times in each block, to be more comparable to the 8 presentations of a single type in runs blocks. Detection of the moth used in the previous runs block may then be compared with ability to detect the moth for which the bird does not have a searching image at various stages within the block.

Finally, it seems important to understand more about the patterns that render a moth cryptic. While asymmetry seemed to have little effect overall, some symmetric patterns were clearly more detectable than others. While the moths that were manipulated in 80% of their pixel locations were identical in their frequency distribution of greyscale values and appeared to have patterns that would render them cryptic on the backgrounds used, the birds found them without difficulty. It is likely that although the overall intensity of the moths was the same, the intensity of certain pixels, or certain regions of the moth wing, were perceived as lighter or darker, due to the intensity of surrounding pixels (Ratliff, 1965). To ensure that the patterns of the two moths presented in chapter 3 closely resembled the patterns found on the backgrounds, the same algorithm used to randomly produce backgrounds was used to create wing patterns. Even then, one moth was more cryptic than the other. It appears that the best way to generate moths that are similar in crypticity is to allow birds to select them (Bond & Kamil, 2002).

Overall, these experiments have demonstrated that degree of similarity between morphs is an important factor in the evolution of prey appearance and that the temporal interval between successive appearances of a single prey type has only small effects on prey detection. They also suggest that asymmetry may influence crypticity of prey under some circumstances, but crypticity cannot easily be quantified and may sometimes conceal pattern symmetry. These experiments also suggest that searching images may have long-lasting effects, and these effects should be investigated.

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FIGURE CAPTIONS

Figure 2A. Varying degrees of difference between moth pairs. Moths at the top of each group were generated by photographing preserved moths, scanning the photographs to create graphics files, and then reducing the images to fit within a 16 pixel by 16 pixel square. Images were converted to grayscale to avoid complications due to bird color vision. Moths below these prototype images were generated by swapping greyscale values at random locations on the prototype moth. Images created by swapping 20% of pixels created moths that were most similar in appearance to the prototype. Moth images created by swapping 80% of pixels in the prototype moth were extremely different in appearance.

Figure 2B. Diagram of an operant box. Birds sat on a perch facing a computer monitor. When the birds correctly detected a moth on the computer screen, the birds pecked at the location in which the moth appeared. A touchscreen device was used to determine where the bird pecked. If the bird pecked the location of a moth image, the stepper motor advanced a feeder, providing a food reward to the bird in a well below the perch.

Figure 2C. Effects of previous detections on accuracy for moth-difference treatment groups.

Figure 2D. Effects of previous detections on accuracy for the 80% difference group.

Moth 1 was created by reducing the size of a photograph. Moth 2 was created by manipulating 80% of the pixels in Moth 1.

Figure 2E. Effects of sequence type on accuracy for the three moth-difference treatment groups.

Figure 2F. Effects of sequence type on parental strain moths (prototypes generated from photographs) in the 80% difference treatment group

Figure 2G. Effects of sequence type on mutant strain moths (generated by manipulating pixels in prototype moths) in the 80% difference treatment group

Figure 2H. Effects of previous experience on non-runs treatment blocks.

Figure 2I. Effects of sequence type on accuracy for moths in the 40% difference group, utilizing data from the first treatment blocks of the session.

Figure 2J. Effects of sequence type on accuracy for moths in the 20% difference group, utilizing data from the first treatment blocks of the session.

Figure 2K. Effects of sequence type on accuracy for moths in the 80% difference group, utilizing data from the first treatment blocks of the session.

Figure 3A. Two moth images are displayed on backgrounds of difficulty levels 0 through 5.

Figure 3B. Diagram illustrating the creation of artificial moth images. A.) A background image used to produce high crypticity for moths in a previous experiment. B.) An 8-pixel wide by 16-pixel high block from such a background is selected. C&D) The selected block of pixels is removed to form a new graphics file. E.) The upper-left and lower-right portions of the block are removed to make the block more "wing-like." F.) The mirror image of the left wing is generated. G) The left and right wing images are combined to form a single moth image. H). The moth image, overlaid on another background image of the same type, produces a cryptic target.

Figure 3C. Effects of background difficulty on mean accuracy, plotted separately for two moth types.

Figure 3D. Effects of background difficulty on response time for positive trials, plotted separately for two moth types

Figure 3E. Effects of sequence type (runs vs. non-runs) and trial position on accuracy.

Figure 3F. Effects of sequence type on reaction times.

Figure 3G. Effects of sequence type (runs of each moth type and non-runs) and trial position on accuracy

Figure 3H. Effects of sequence type (runs of each moth type and non-runs) and trial position on response time

Figure 3I. Effects of 0, 20, and 60 second delays on accuracy during the following positive trial.

Figure 3J. Effects of 0, 20, and 60 second delays on accuracy, plotted separately for two moth types.

Figure 3K. Effects of 0, 20, and 60 second delays on response time.

Figure 3L. Effects of 0, 20, and 60 second delays on response time, plotted separately for the two moth types.

Figure 4A. Moth images used to compare crypticity of symmetric and asymmetric moths. Moths on the top row were created by utilizing patterns created by an algorithm used to generate backgrounds in a previous study; left and right halves are mirror images. In addition to these moths, each bird was also exposed to 6 asymmetric moths. Asymmetrical moths were created by combining left and right halves of two different symmetrical targets.

Figure 4B. Effects of prey symmetry and background difficulty level on accuracy

Figure 4C. Effects of prey symmetry and background difficulty level on response time

Figure 4D. Effects of prey symmetry and background difficulty level on accuracy

Figure 4E. Effects of prey symmetry and background difficulty level on response time

Figure 4F. Effects of background on accuracy during negative trials during testing of ability to detect symmetric and asymmetric moths.

Figure 4G. Moth images used in the "virtual prey" study. Moths in the top row were always present in the population. Infrequently, novel pairs of moths (one symmetric, the other highly asymmetric) were introduced into the population in small numbers.

Figure 4H. Changes in density of each moth type in the population over time. After 30 days of searching for only three moth types, novel symmetric and asymmetric moth types (Moth Pair 1) were introduced in small numbers and allowed to increase in numbers as a function of detection.

Figure 4I. Changes in density of novel symmetric and asymmetric moths.

Figure 2A

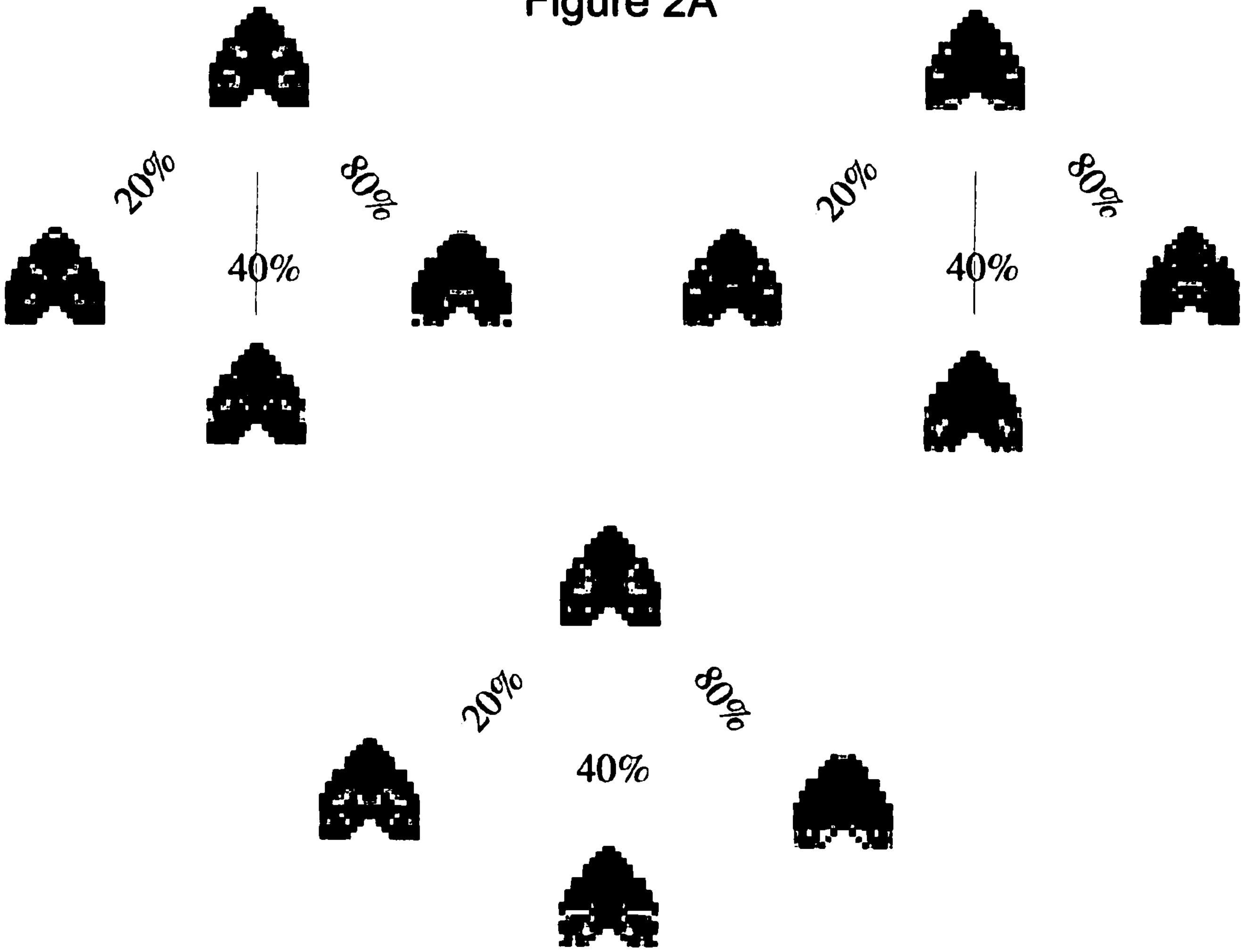


Figure 2B

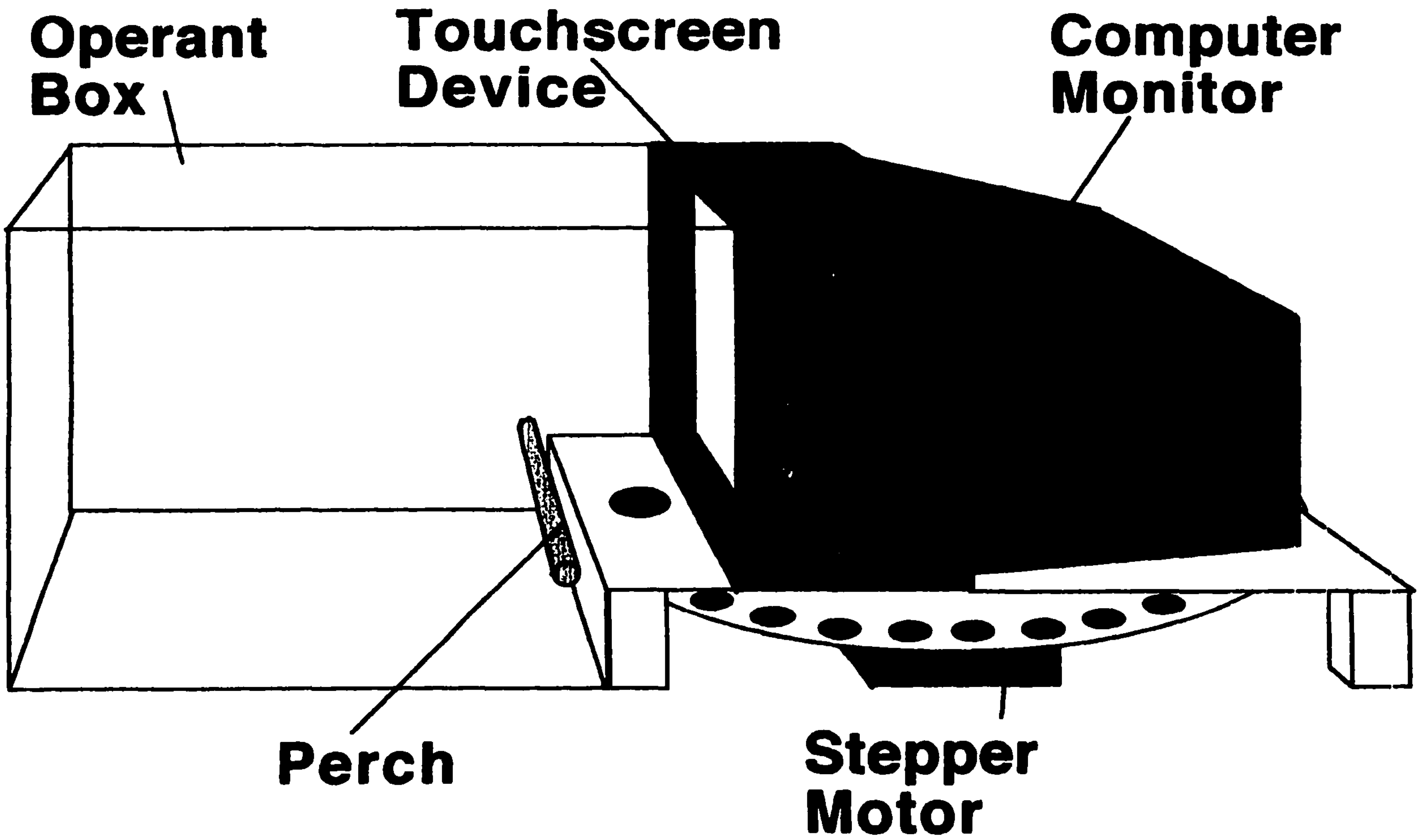

Operant
Box
Touchscreen
Device
Computer
Monitor
Perch
Stepper
Motor

Figure 2C

Effect of NPD on Accuracy

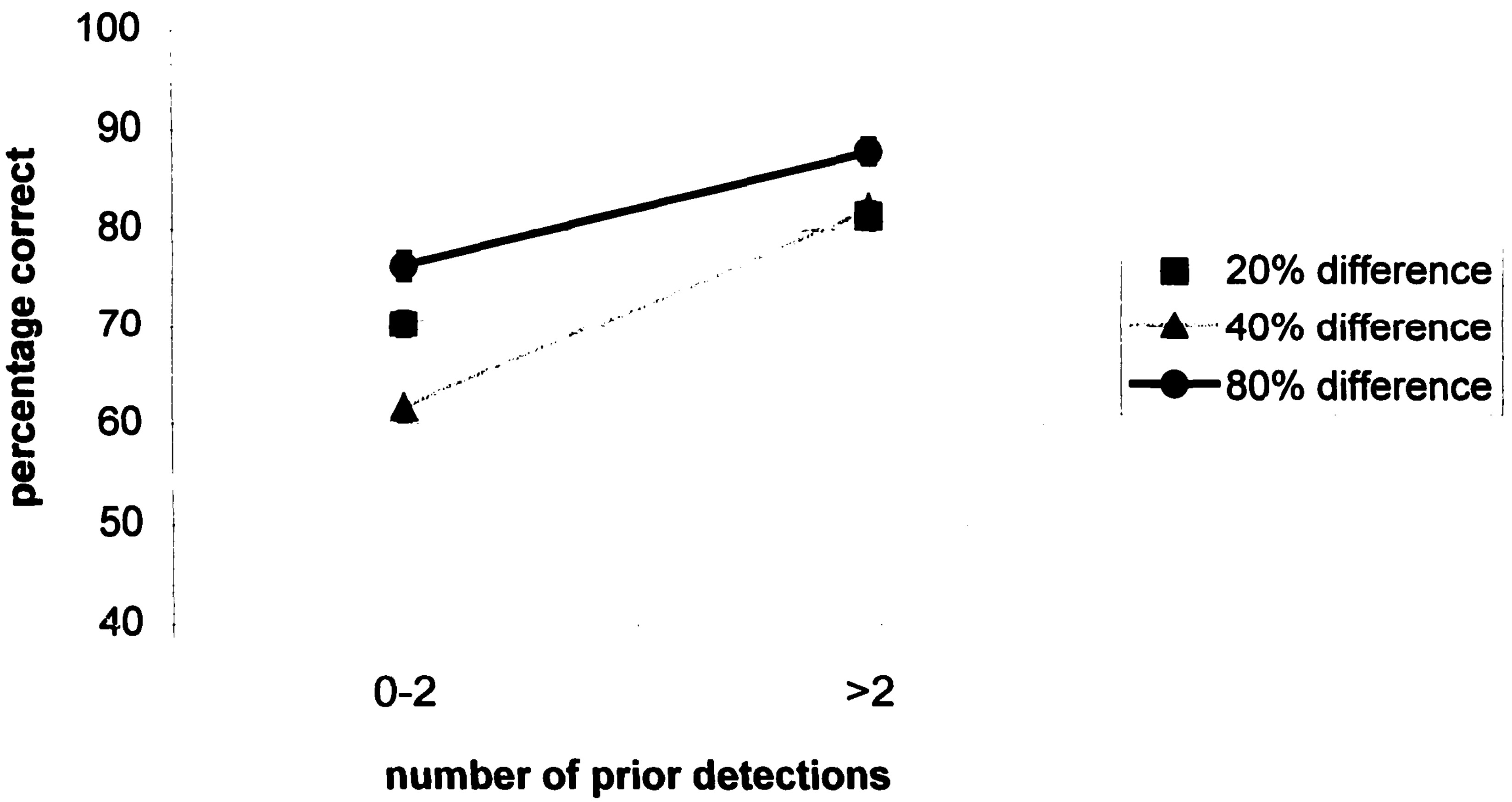


Figure 2D

NPD vs Percentage Correct for Moths 80% Different

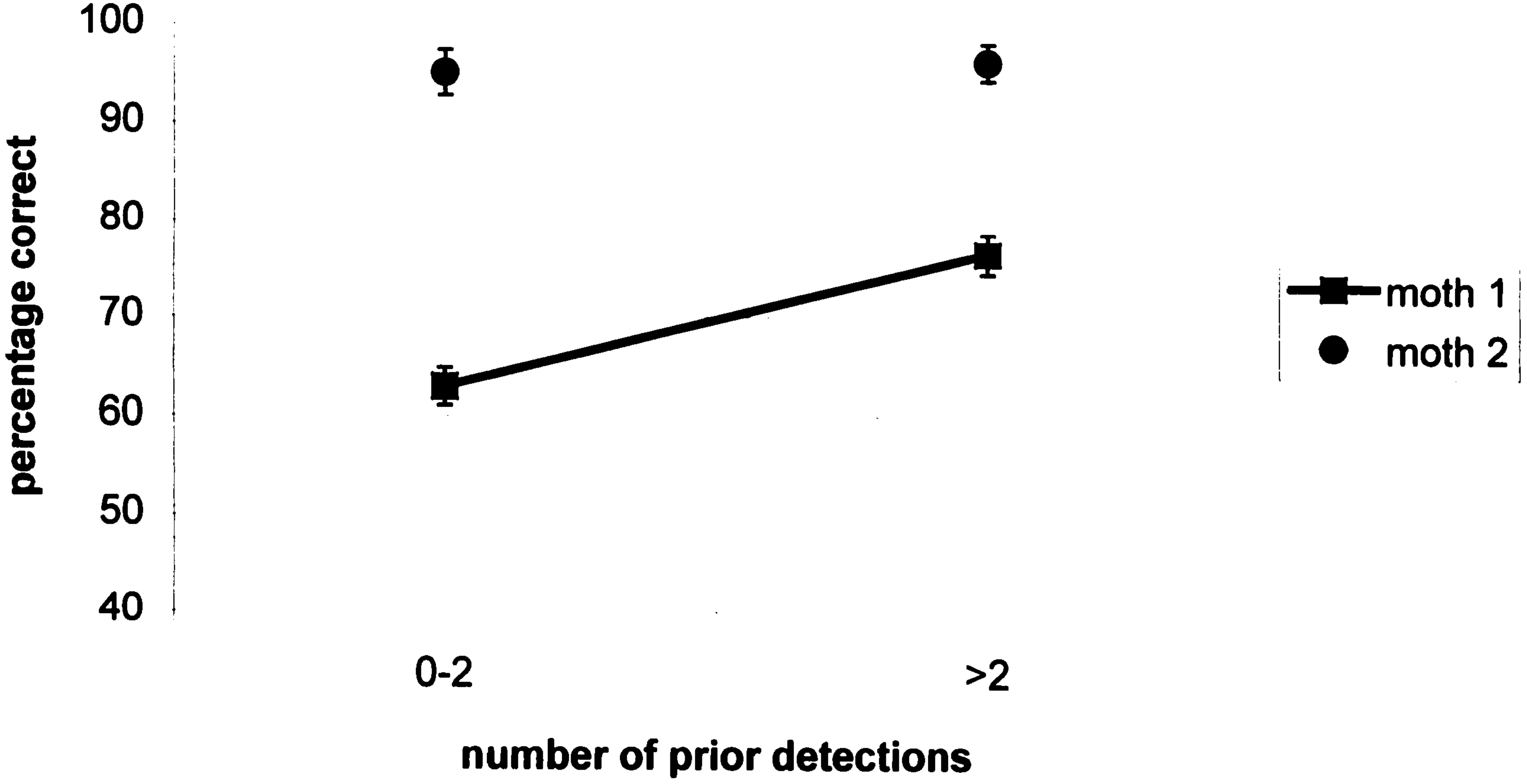


Figure 2E

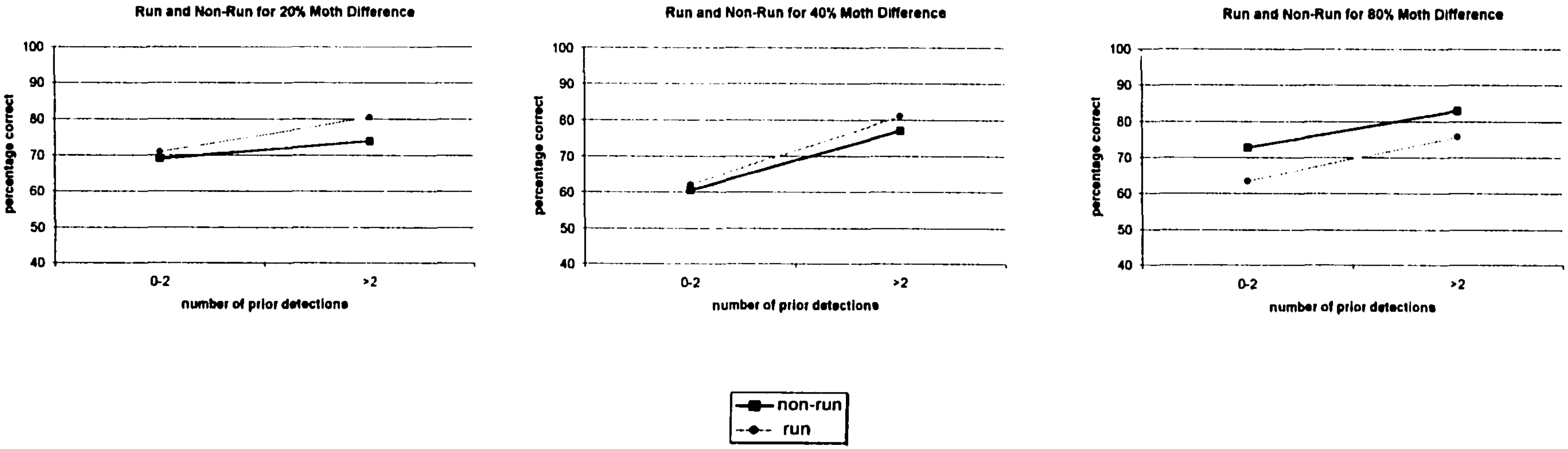

Run and Non-Run for 20% Moth Difference
Run and Non-Run for 40% Moth Difference
Run and Non-Run for 80% Moth Difference
percentage correct
100
90
80
70
60
50
40
0-2
>2
number of prior detections
non-run
run

Figure 2F

Run and Non-Run of Parental Strain Moths in 80% Difference Treatment

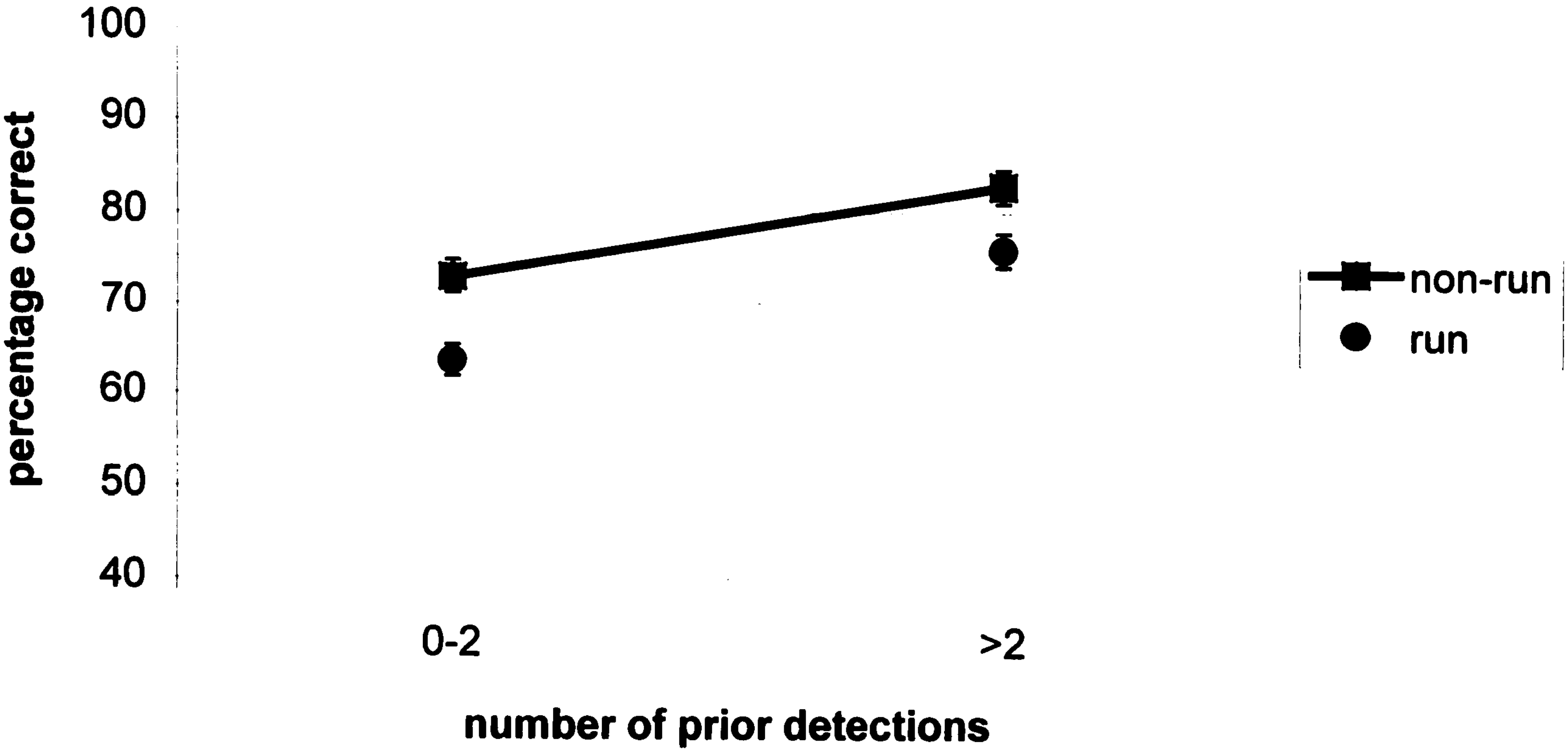


Figure 2G

Run and Non-Run of Mutant Moths in 80% Difference Treatment

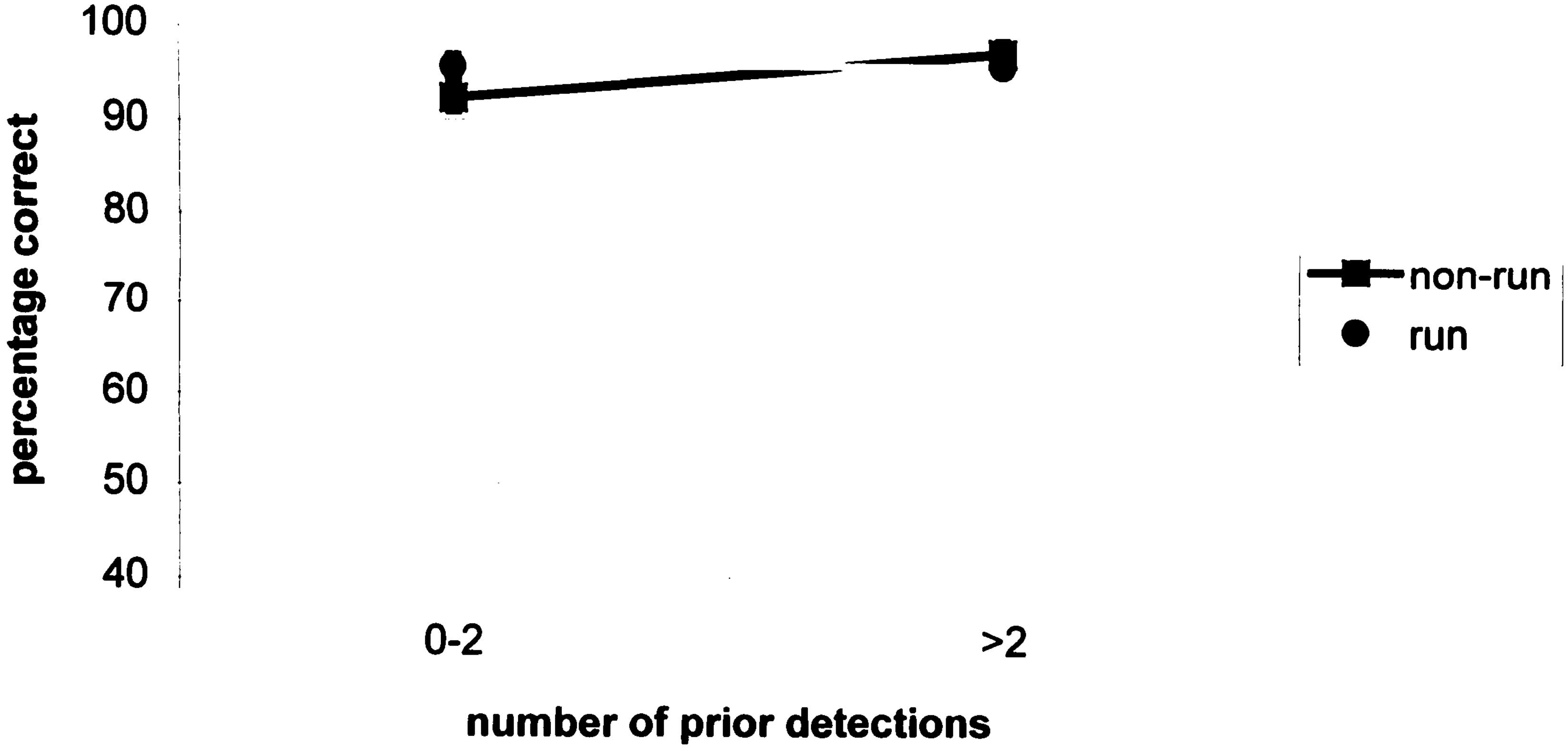


Figure 2H

Accuracy on Non-Runs as a Function of Previous Experience

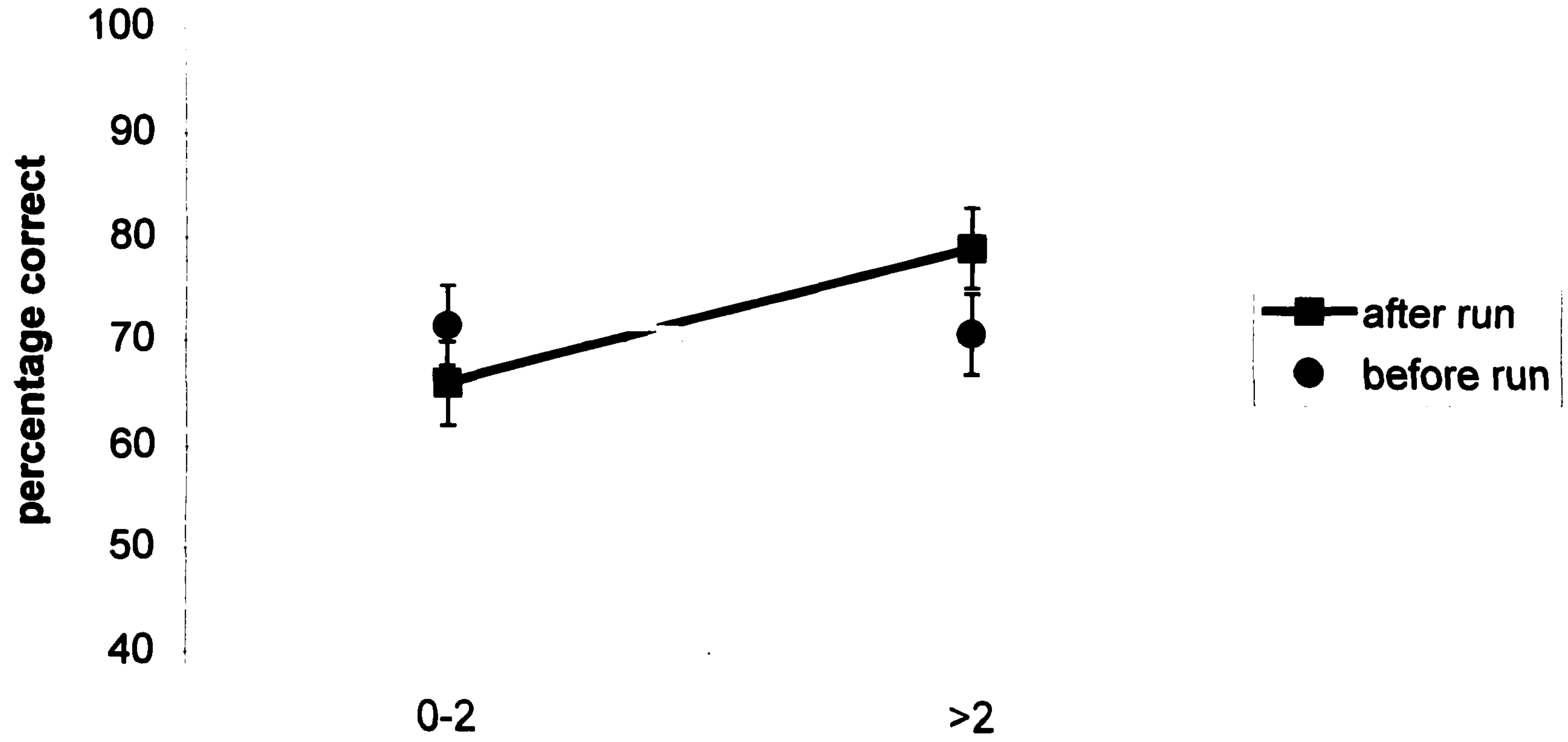


Figure 2I

Runs and Non-Runs for 40% Moth Difference
(first treatment blocks of the session only)

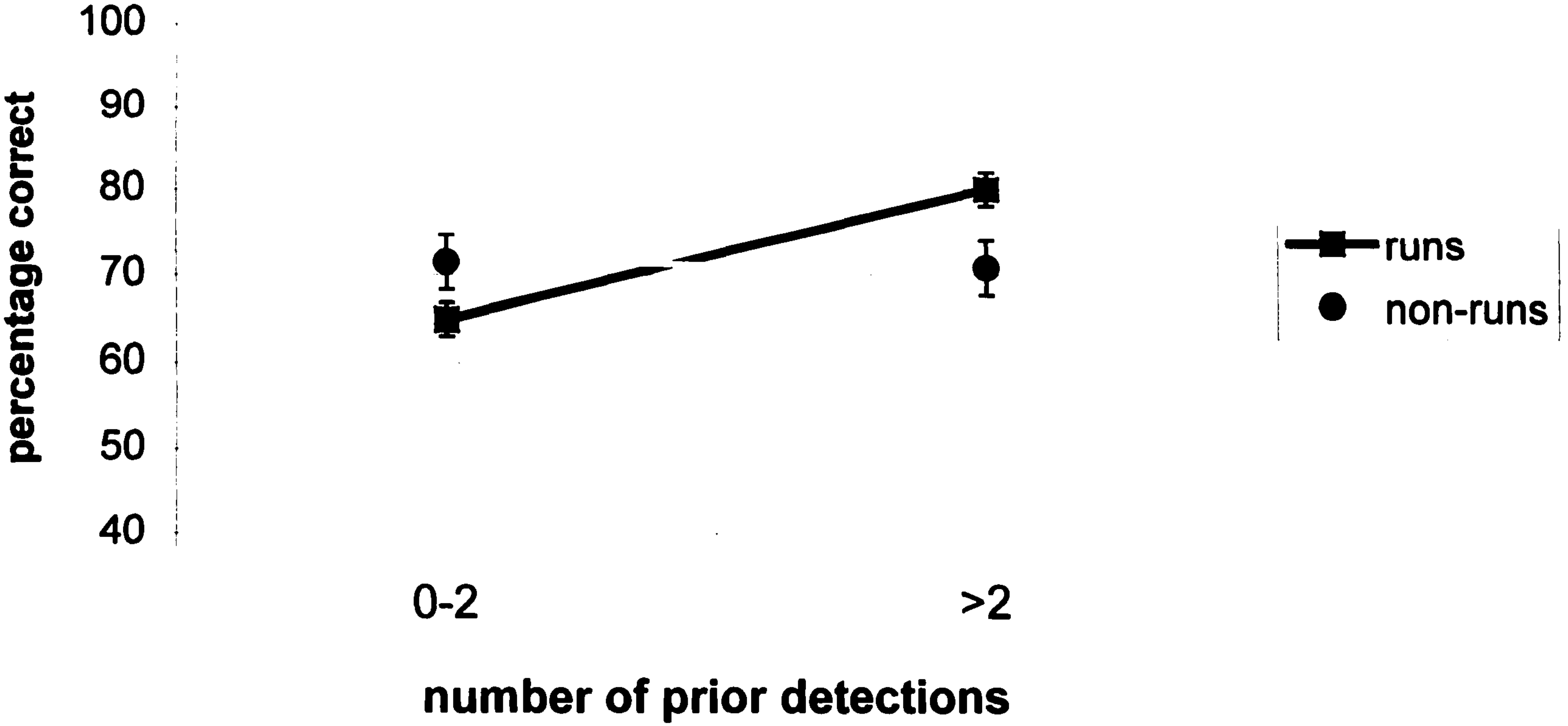


Figure 2J

Runs and Non-Runs for 20% Moth Difference
(first treatment blocks of the session only)

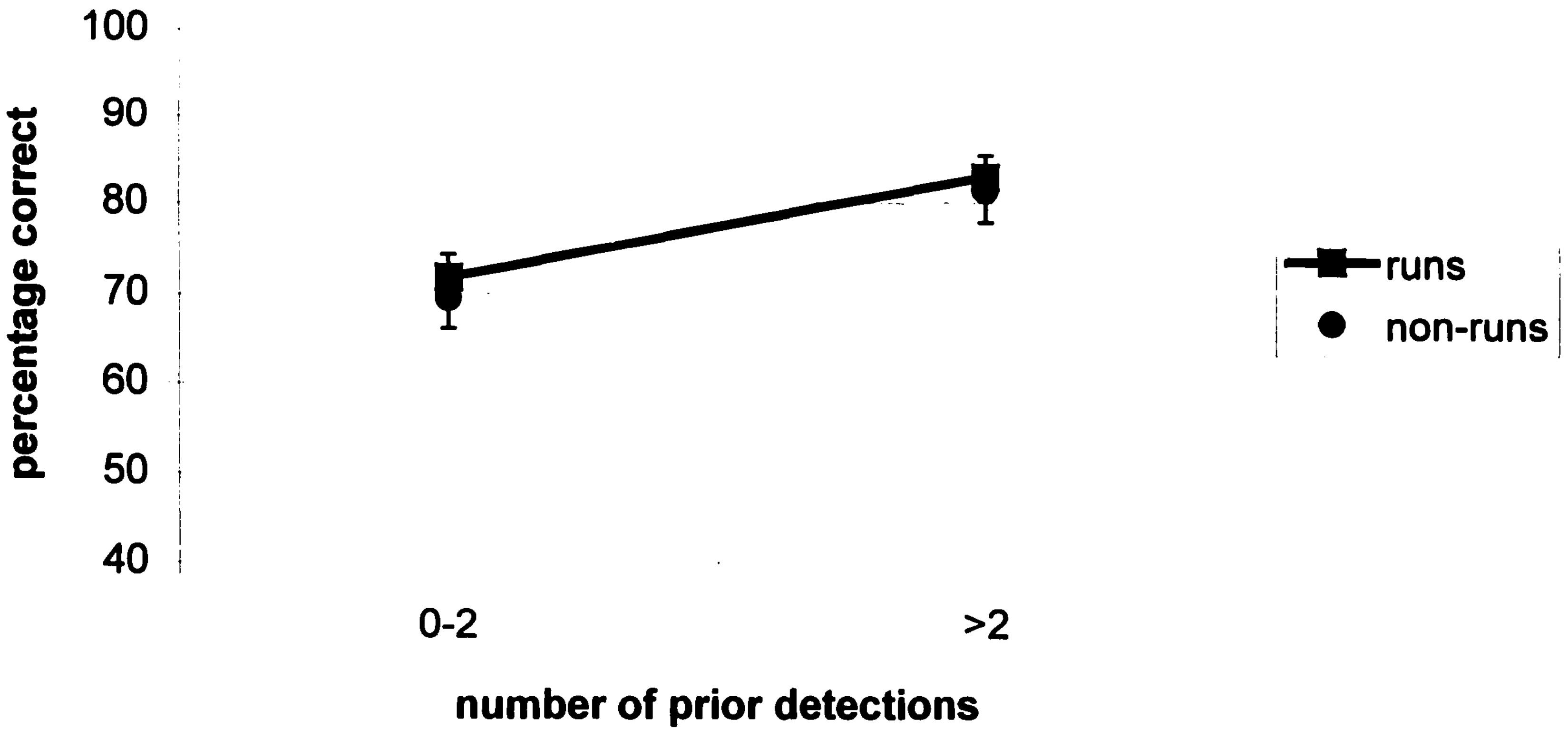


Figure 2K

Runs and Non-Runs for 80% Difference
(first treatment blocks of the session only)

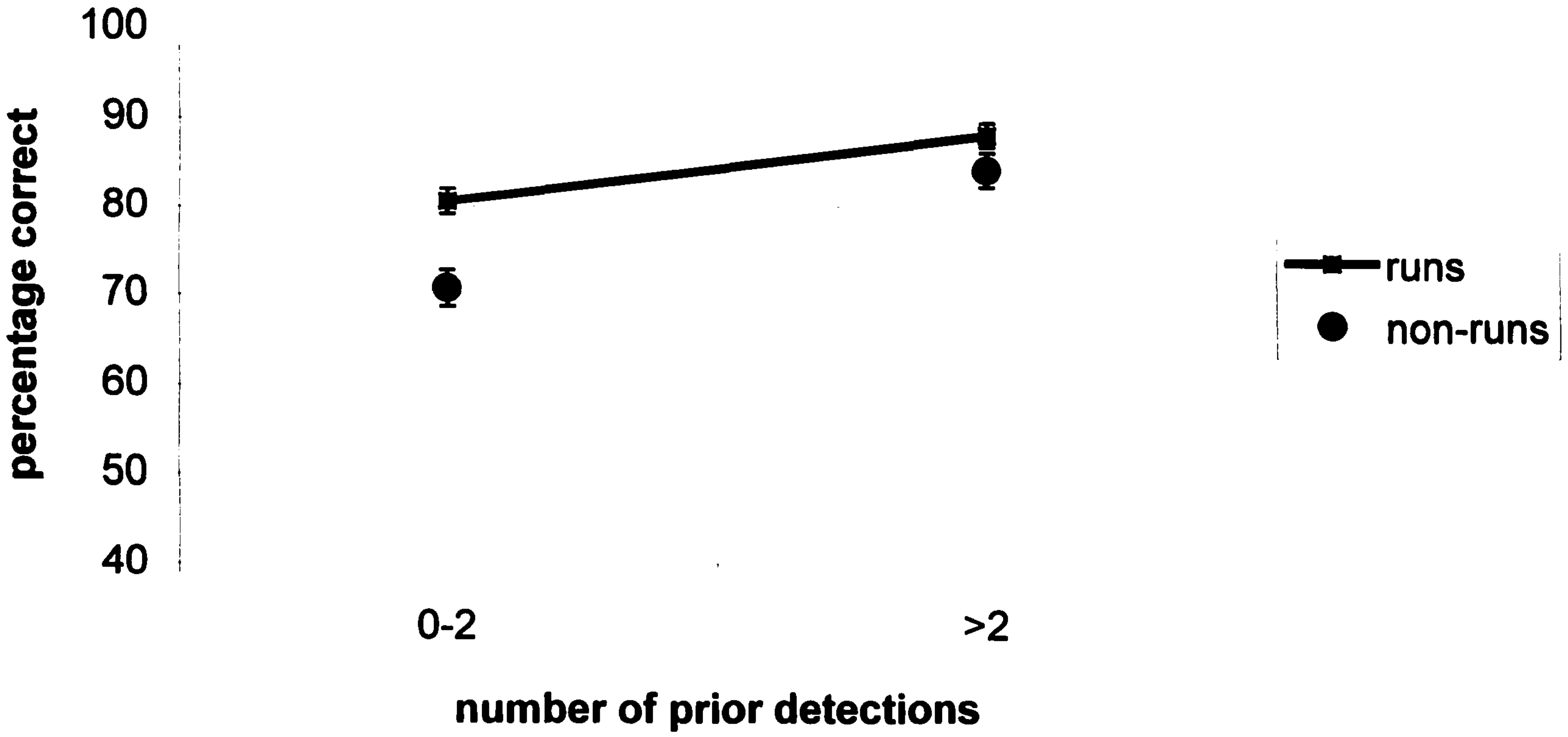


Figure 3A

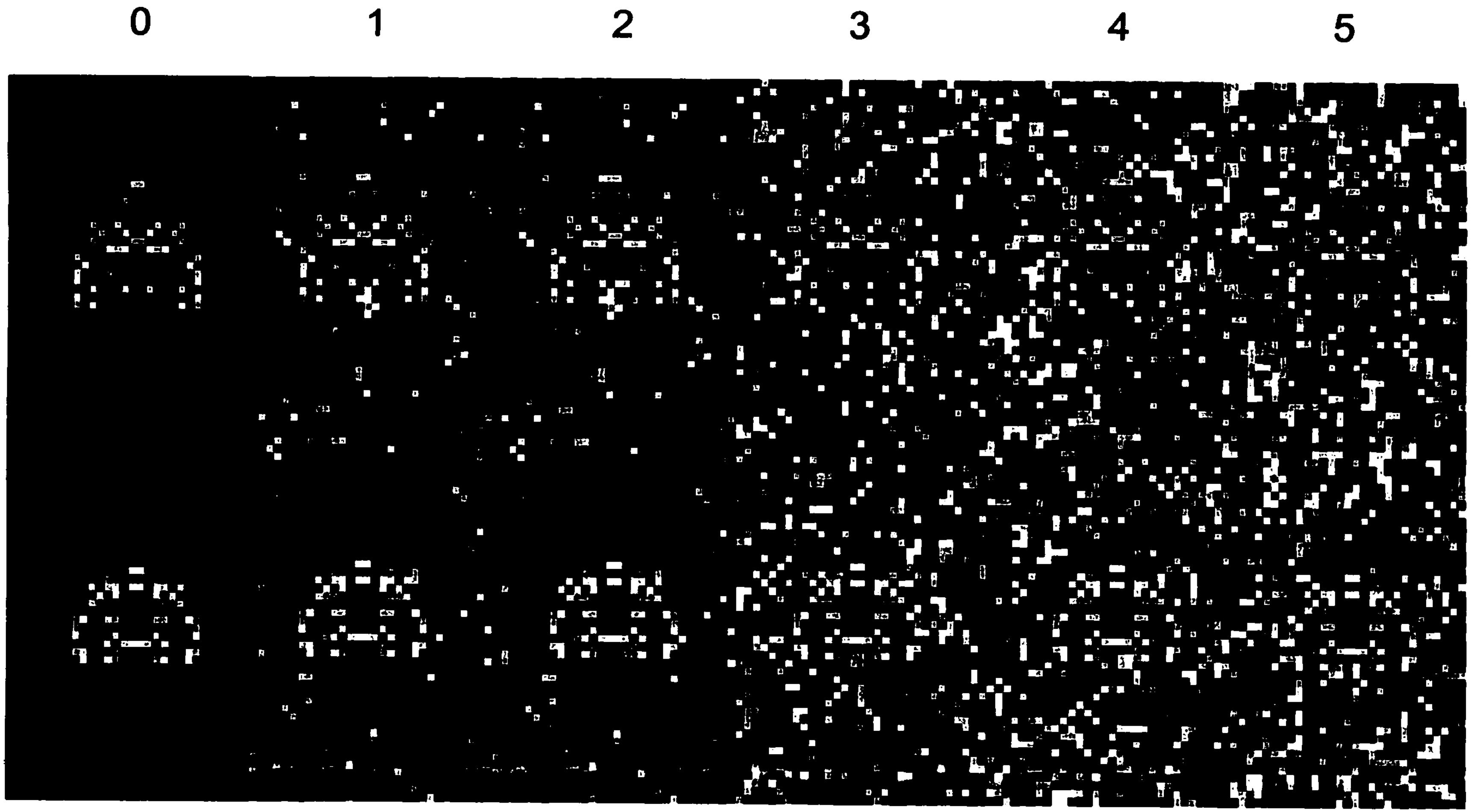
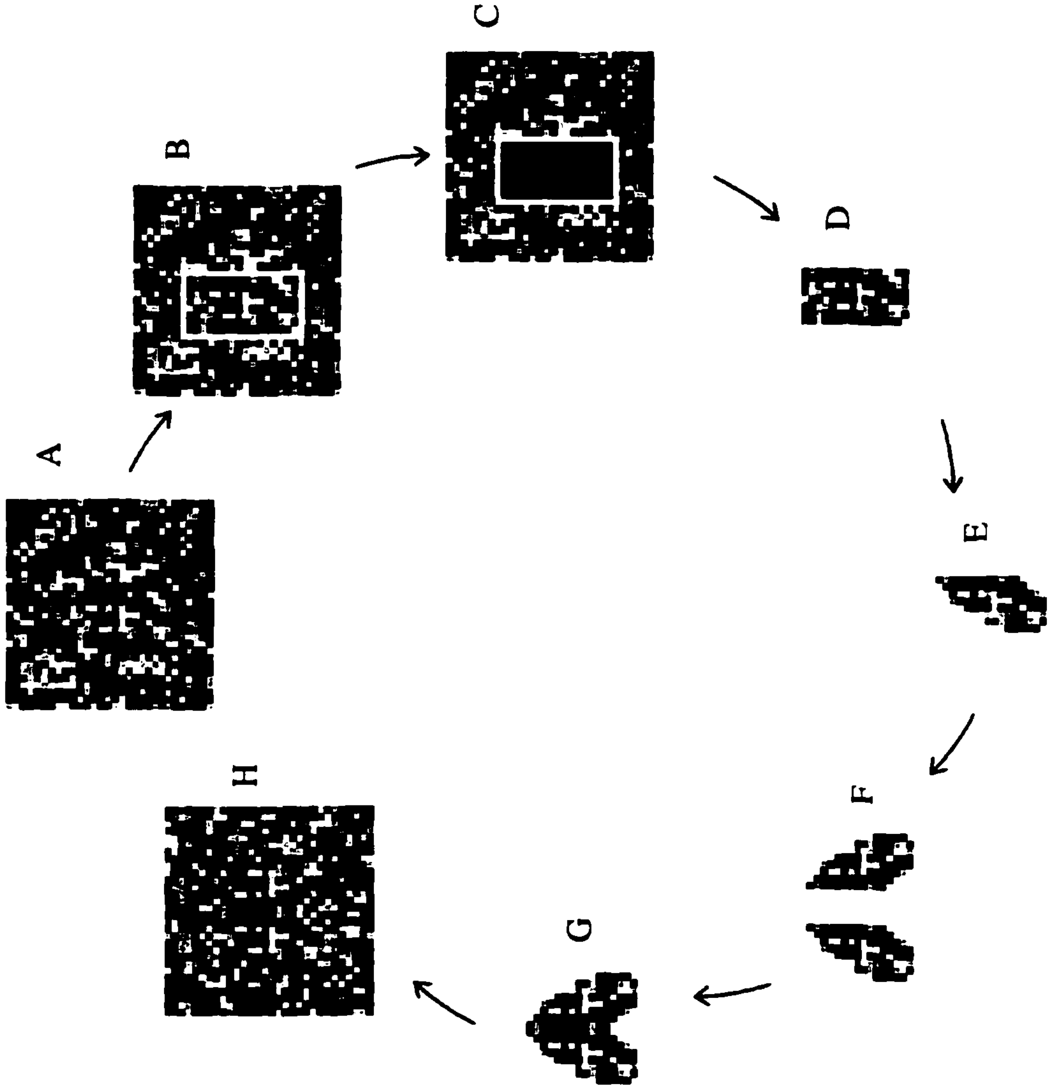


Figure 3B



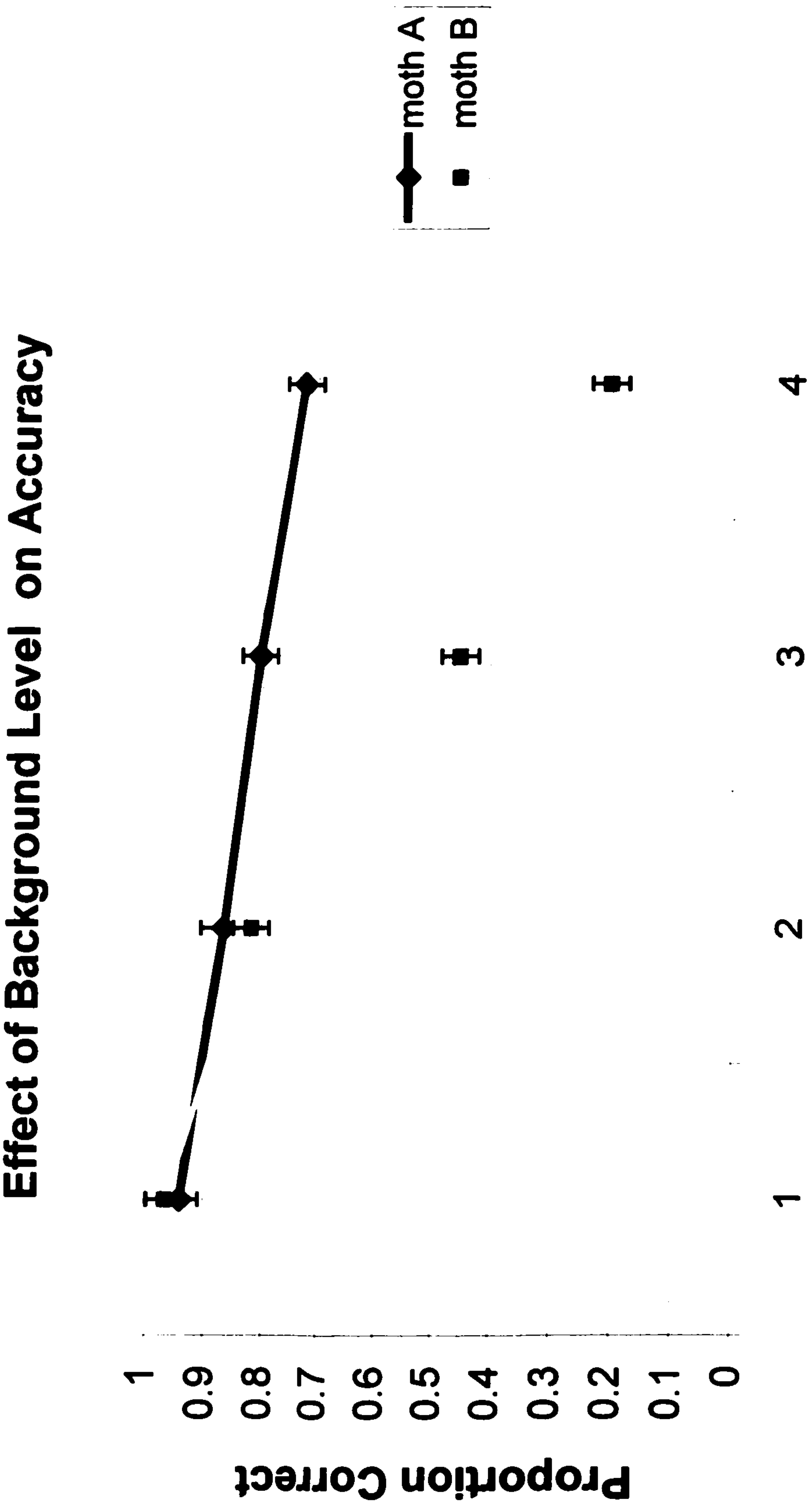


Figure 3C

Effect of Background Level on Accuracy

Figure 3D

Effect of Background on Reaction Time

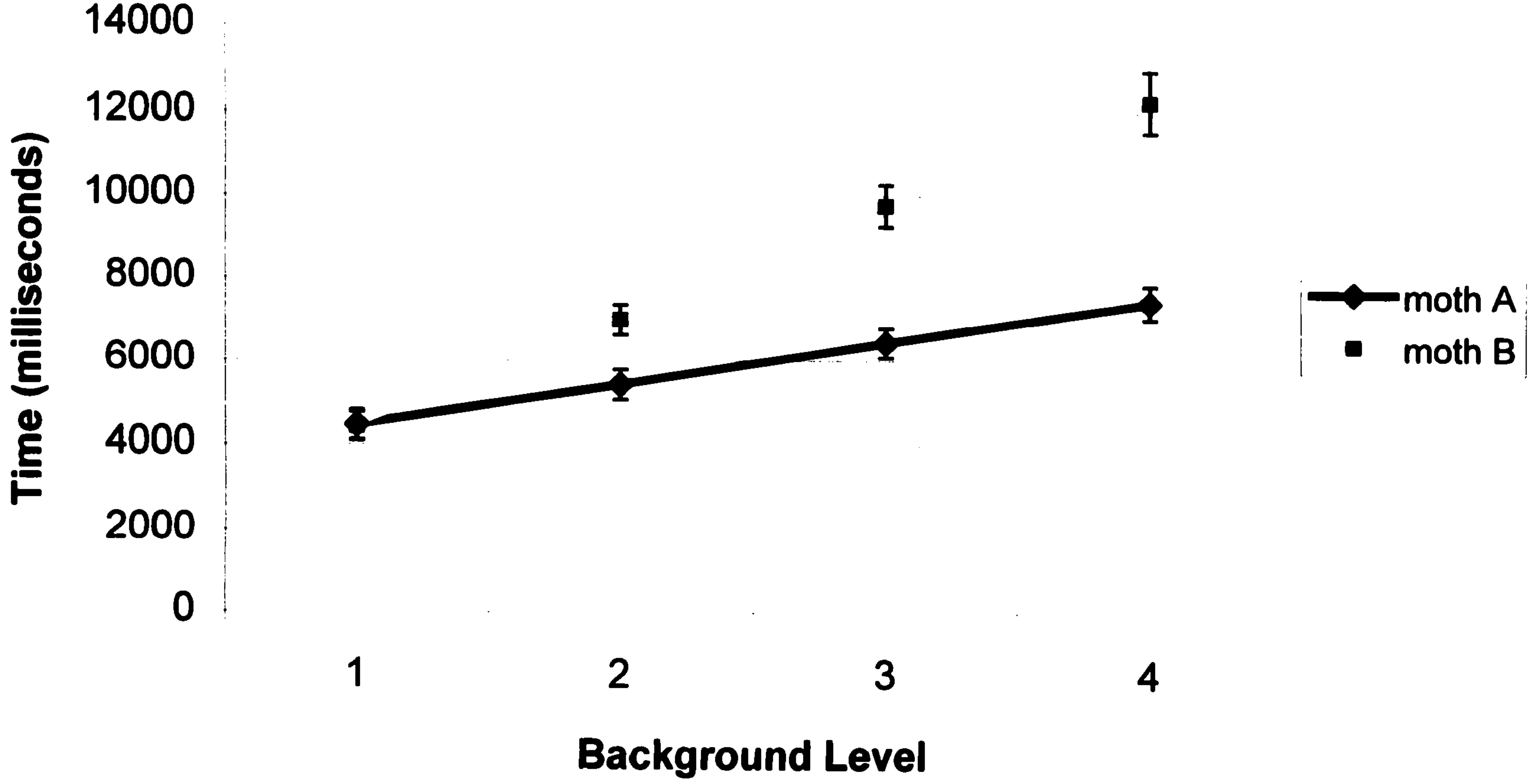


Figure 3E

Effect of Sequence Position on Accuracy

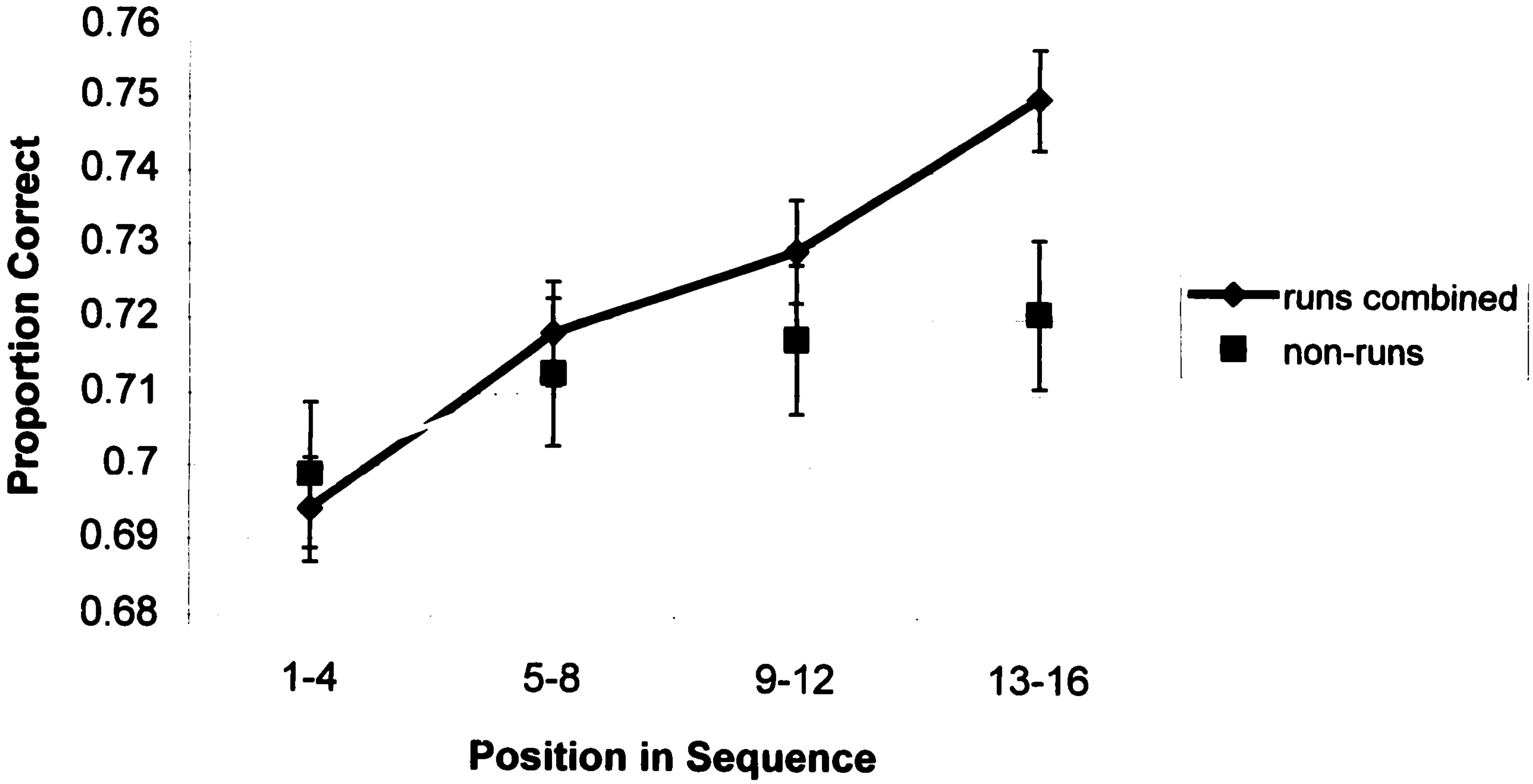


Figure 3F

Effect of Sequence Position on Reaction Time

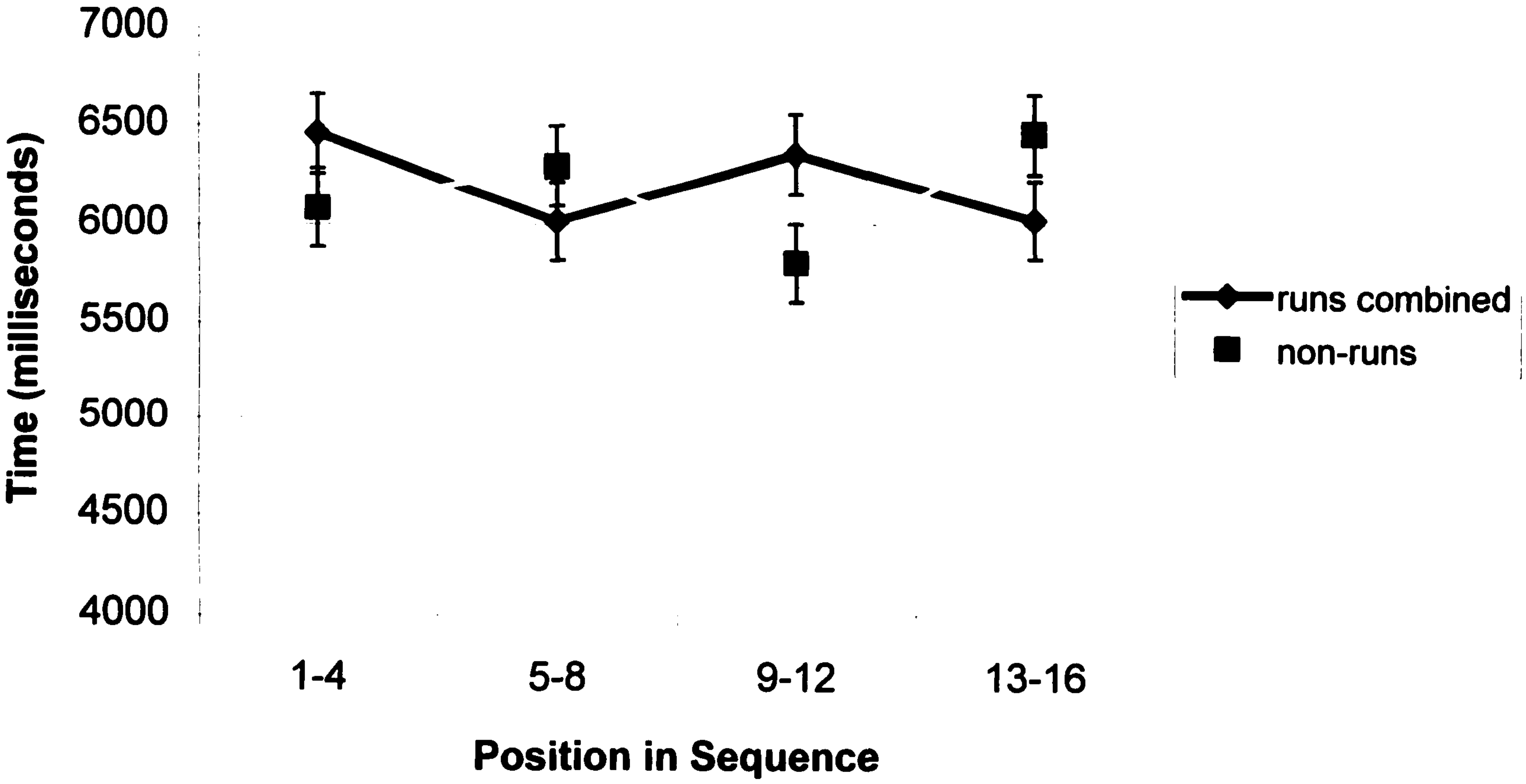


Figure 3G

Effect of Sequence Position on Accuracy for Negatives

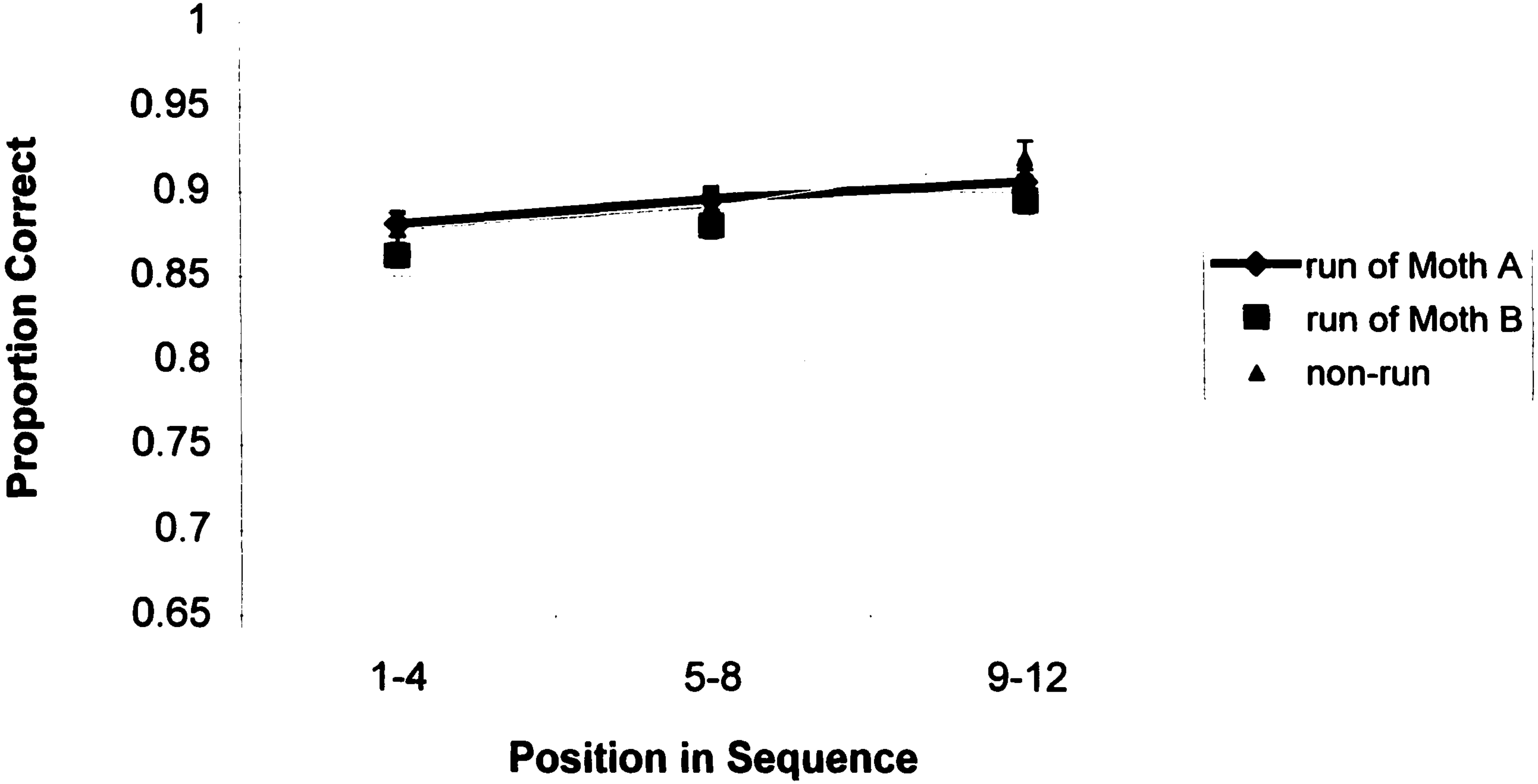


Figure 3H

Effect of Sequence Position on Reaction Time for Negatives

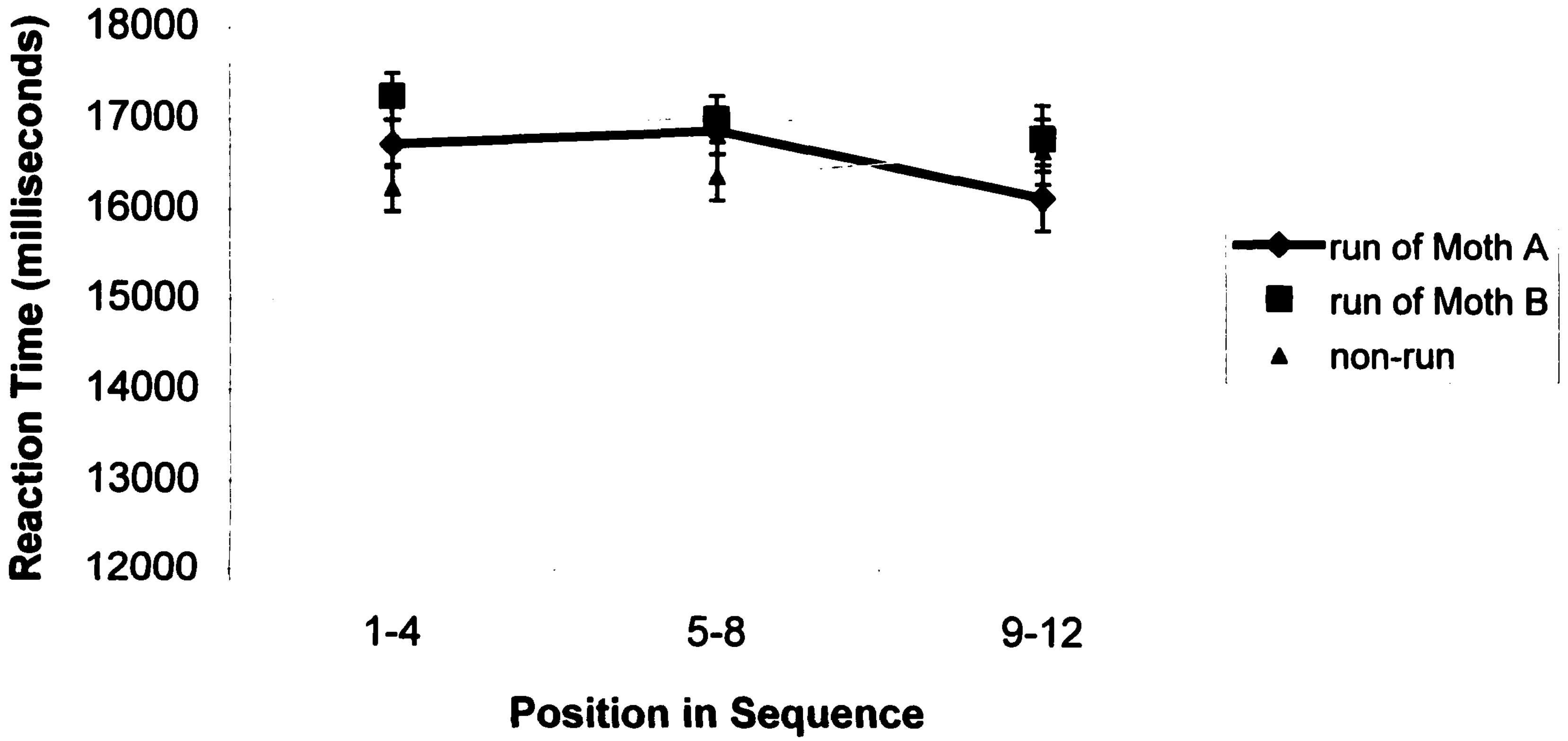


Figure 3I

Effect of Inter-Prey Interval on Accuracy

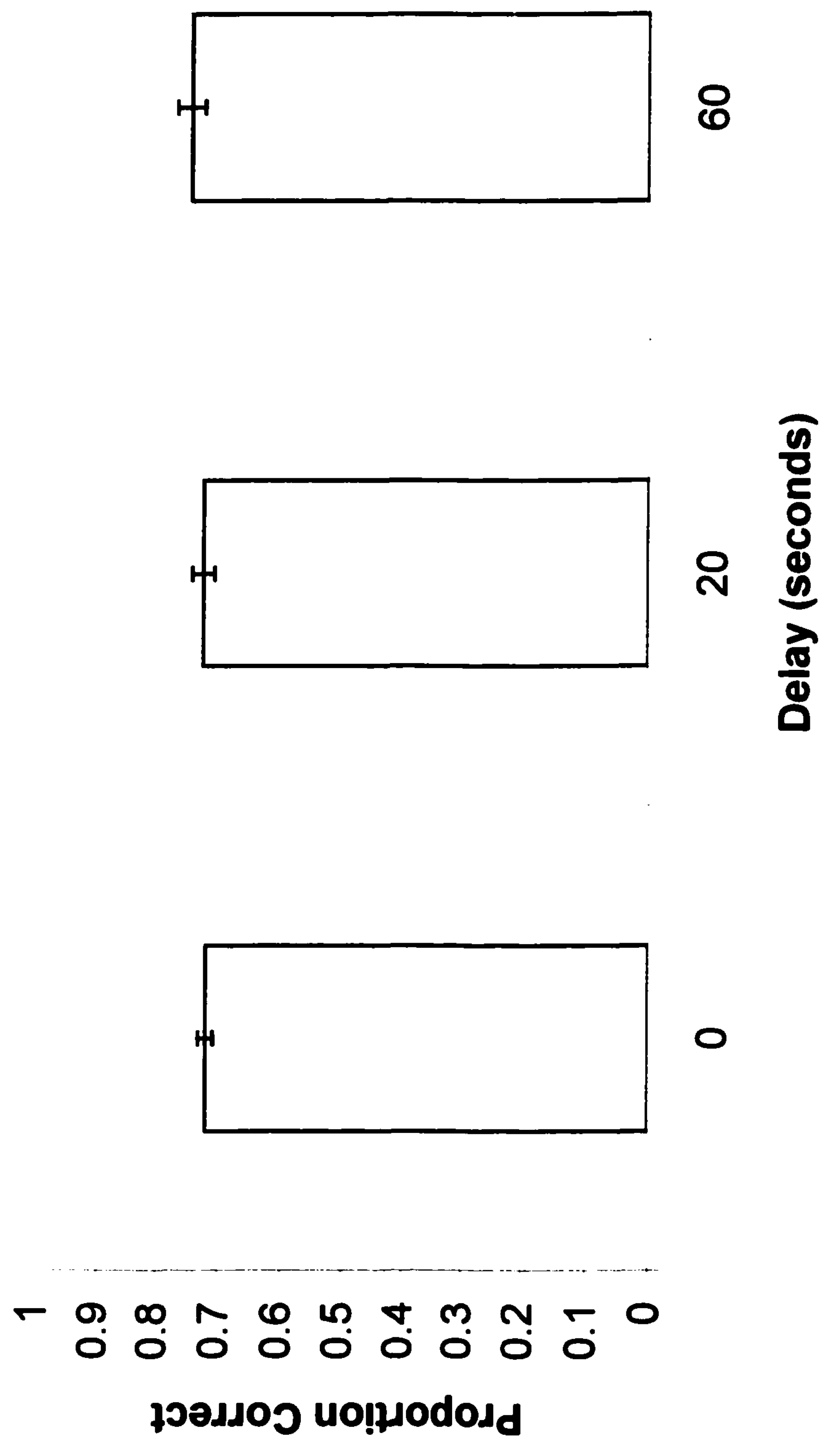


Figure 3J

Effect of Delay on Accuracy

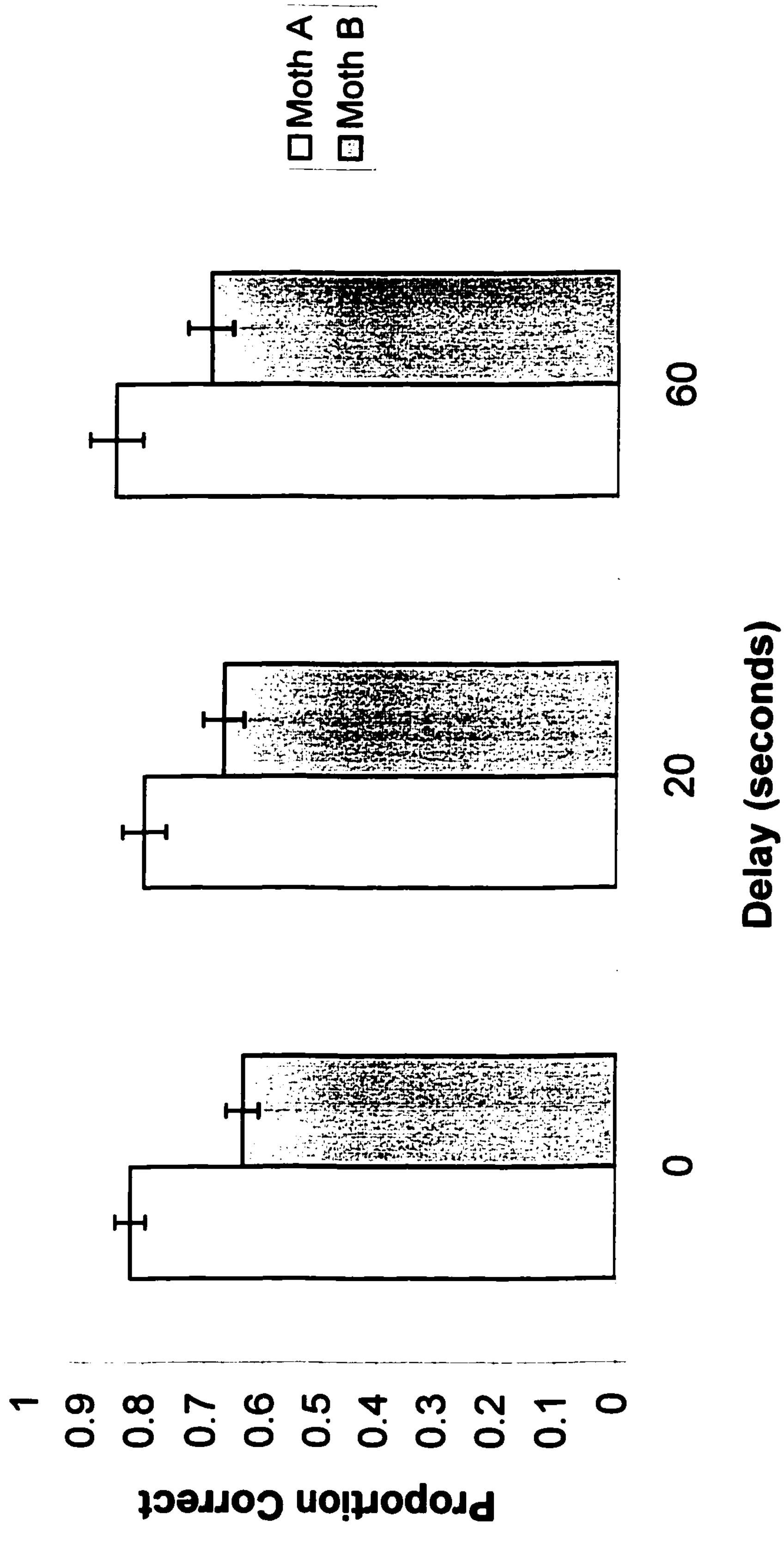


Figure 3K

Effect of IPI on Reaction Time

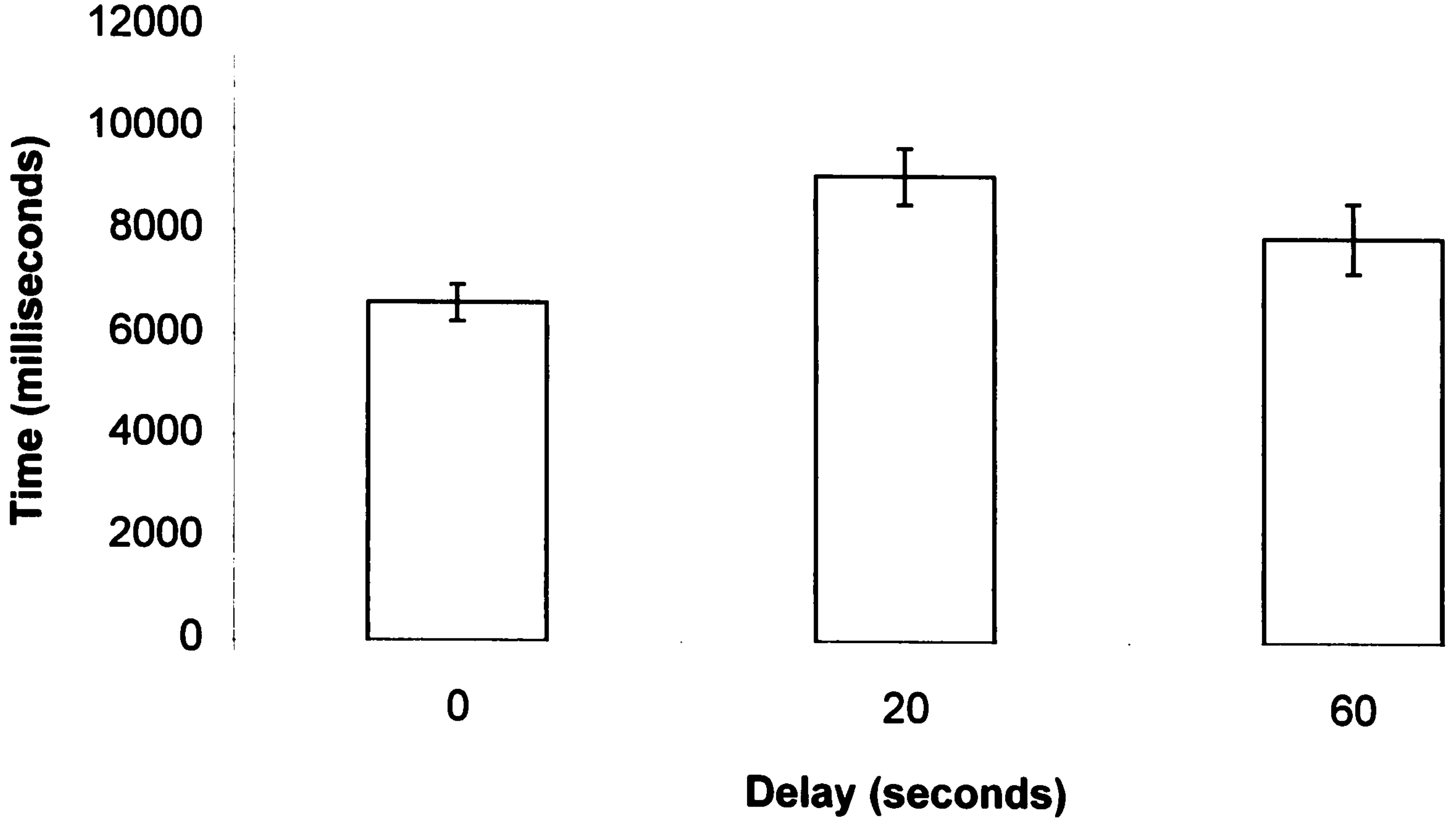


Figure 3L

Effect of Delay on Reaction Time

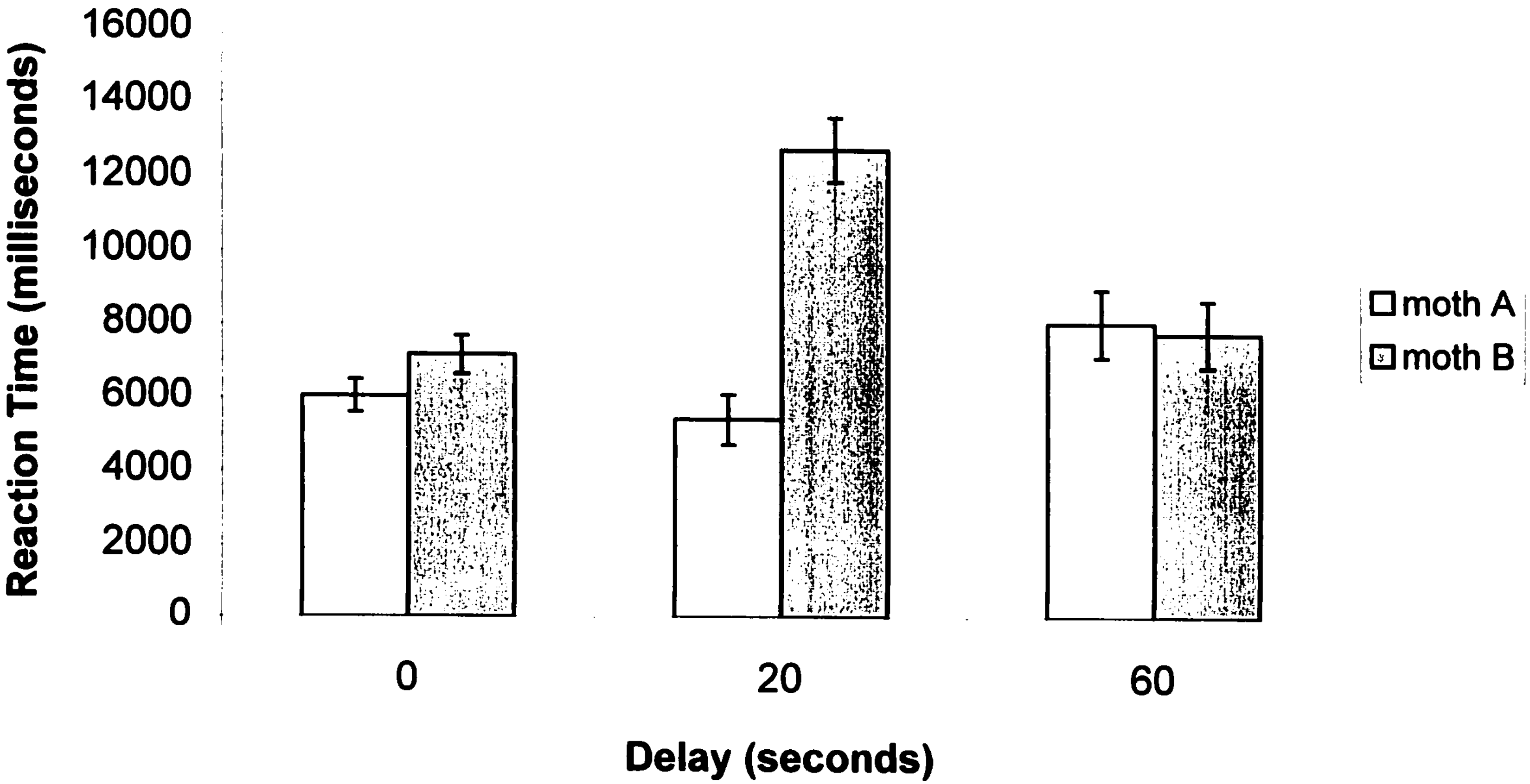


Figure 4A

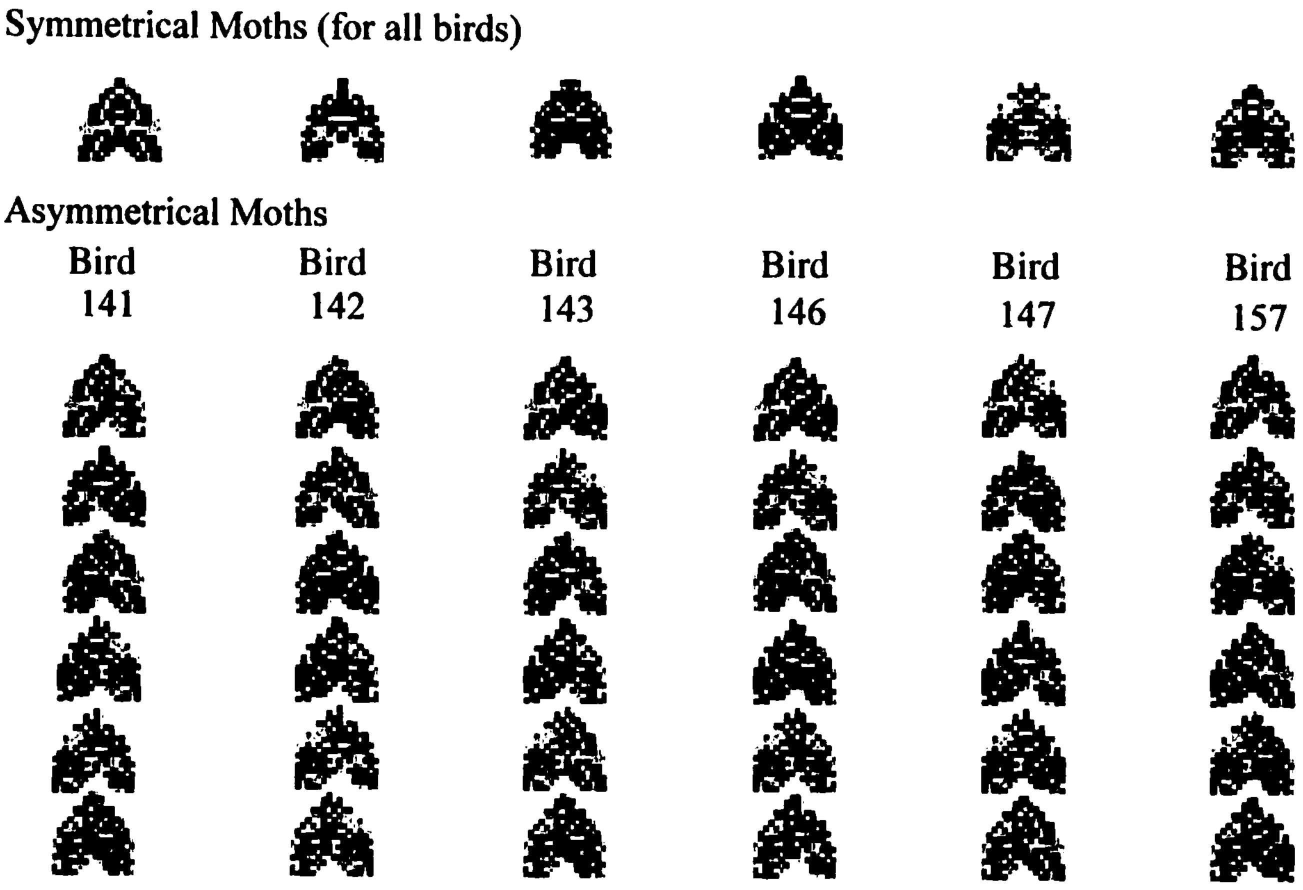

Symmetrical Moths (for all birds)
Asymmetrical Moths
Bird 141
Bird 142
Bird 143
Bird 146
Bird 147
Bird 157

Figure 4B

Effects of Symmetry on Accuracy

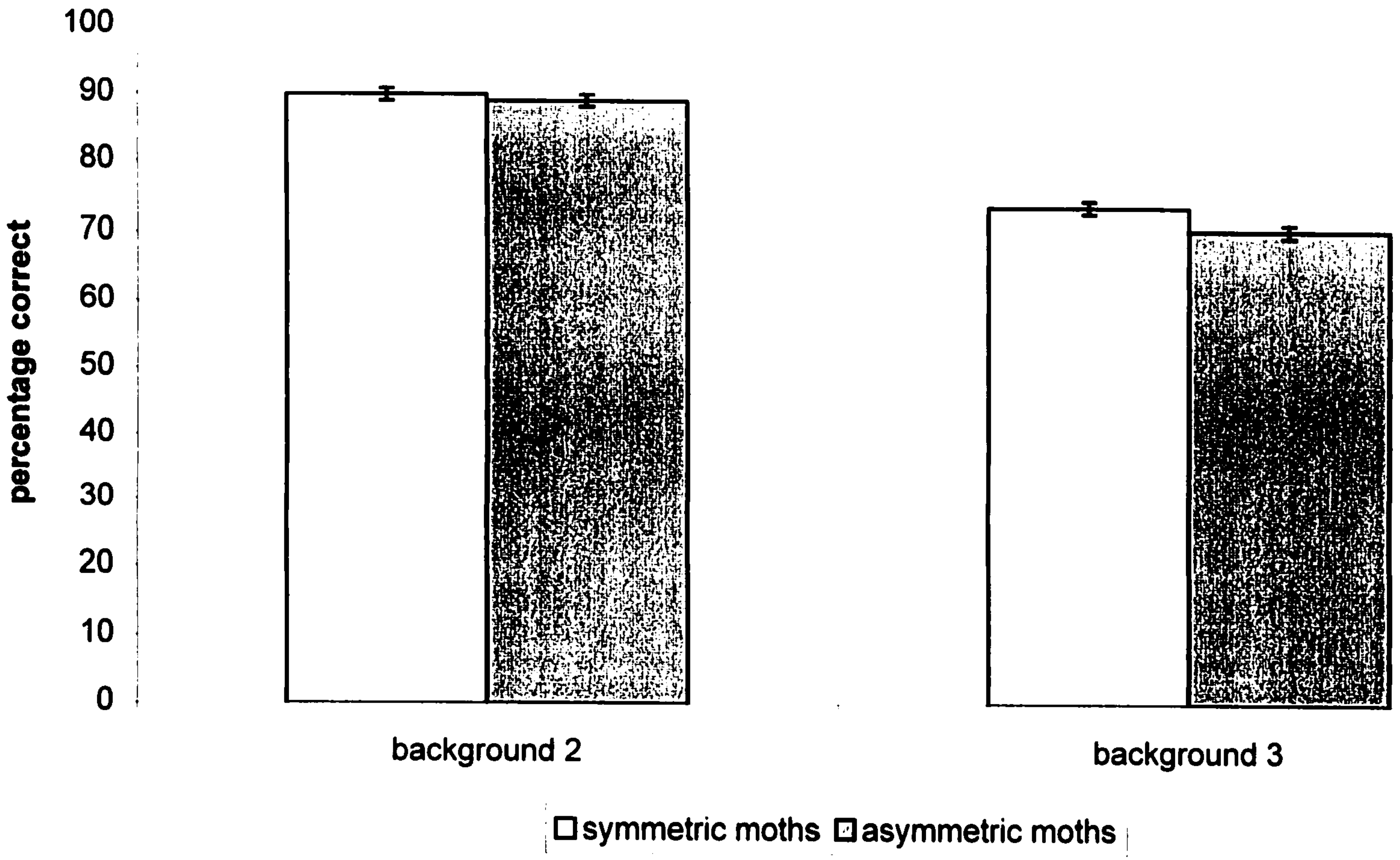


Figure 4C

Effect of Symmetry on Reaction Time

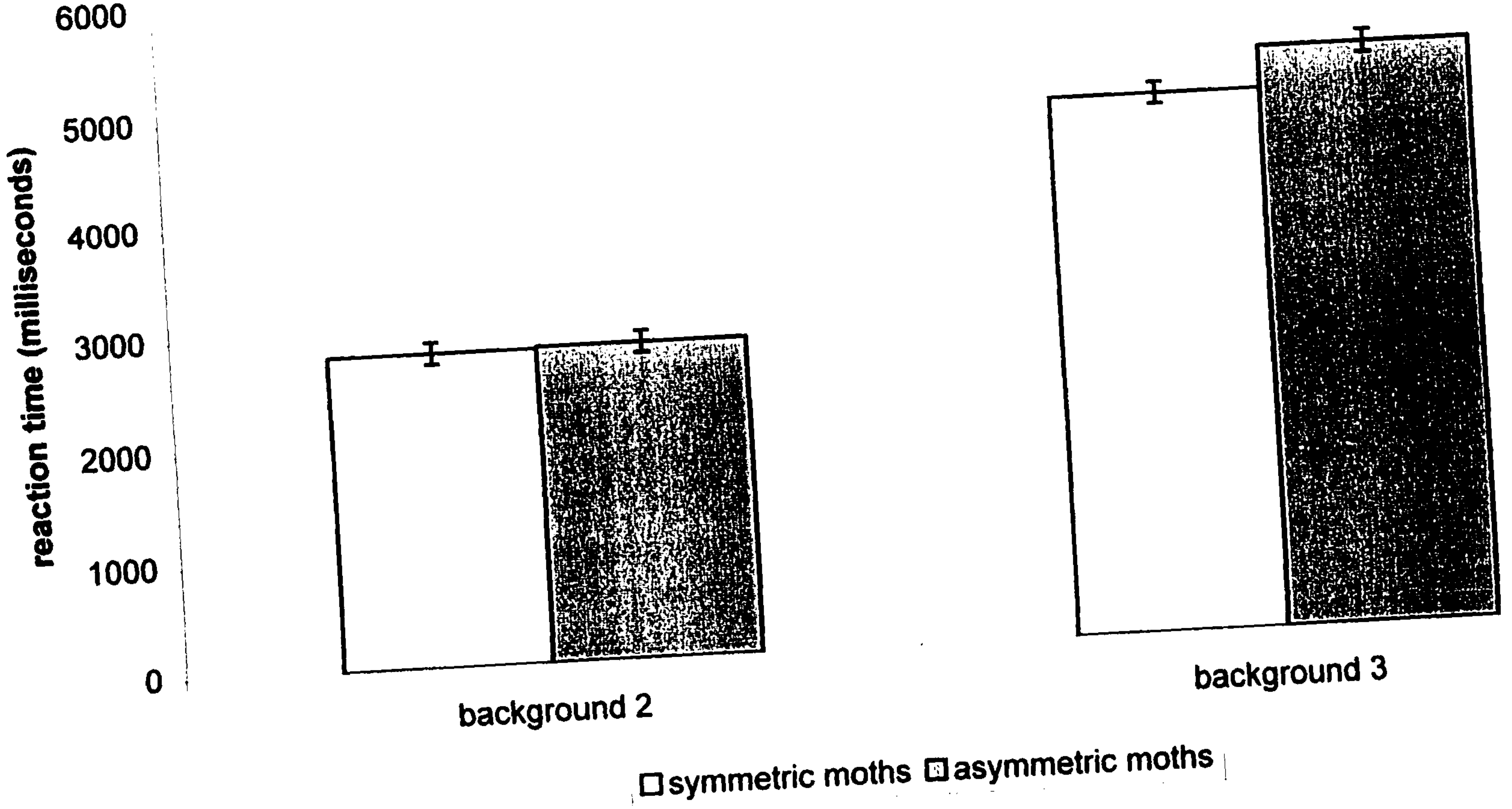


Figure 4D

Effect of Symmetry on Accuracy

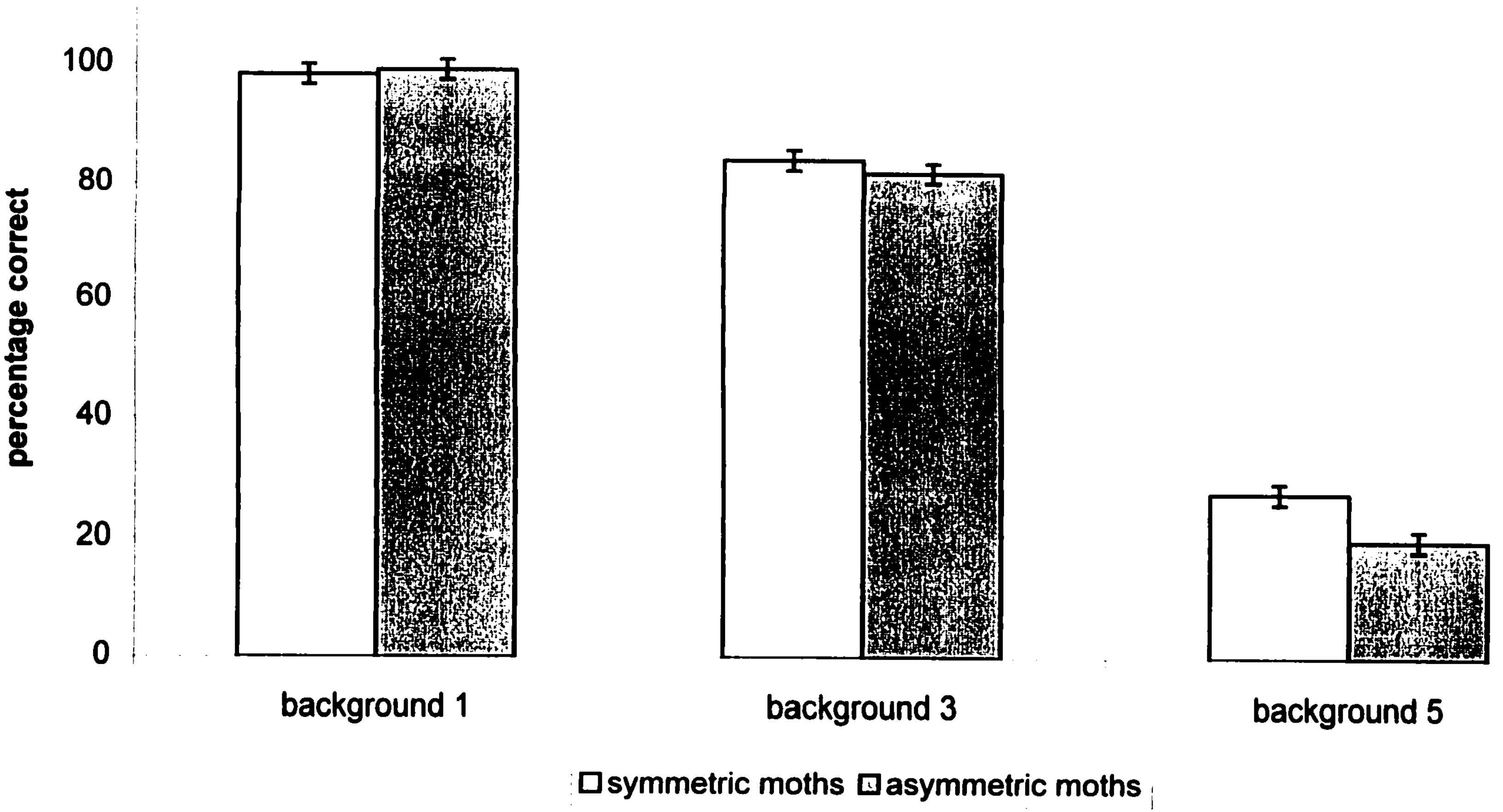


Figure 4E

Effect of Symmetry on Reaction Time

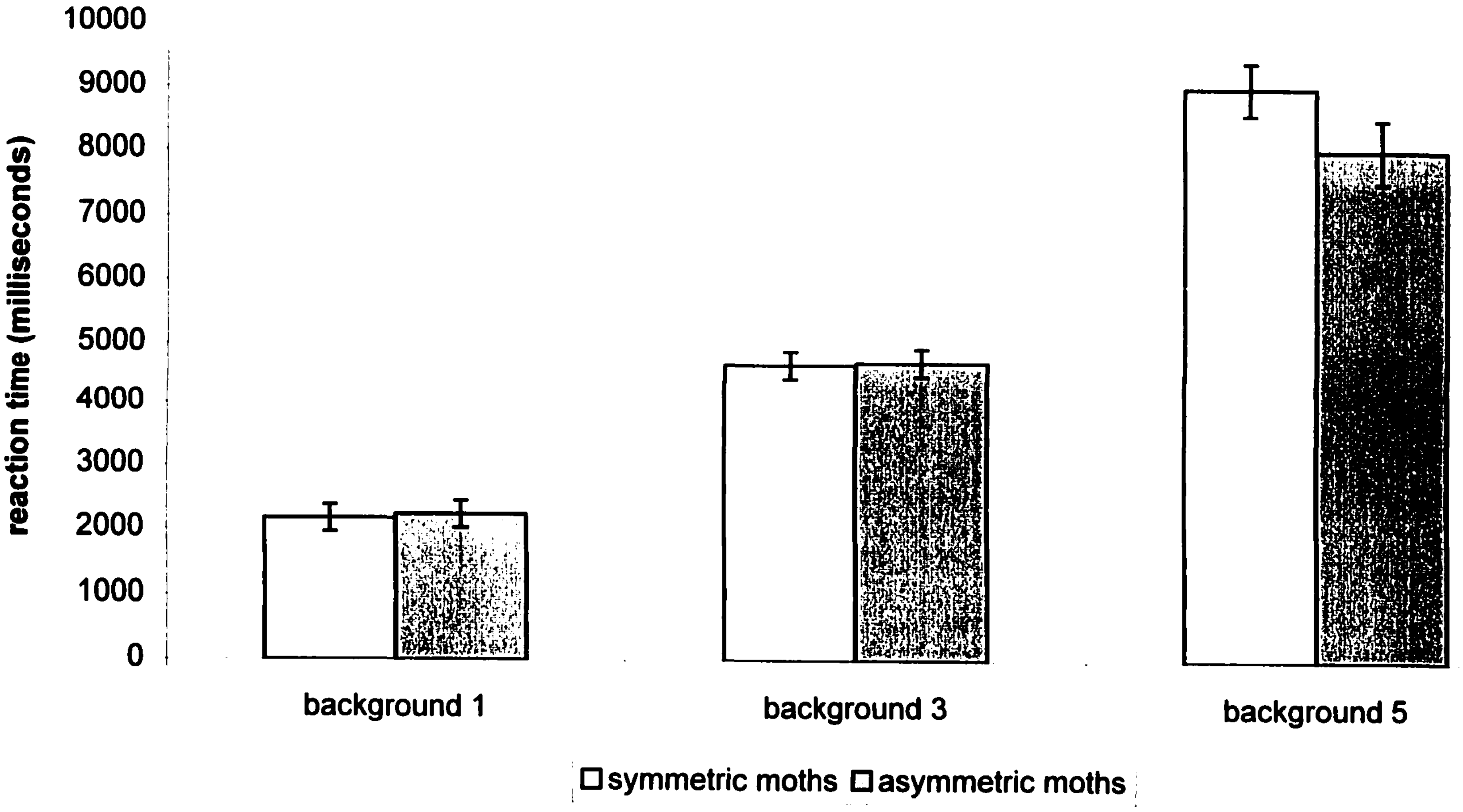


Figure 4F

Effect of Background on Accuracy During Negative Trials

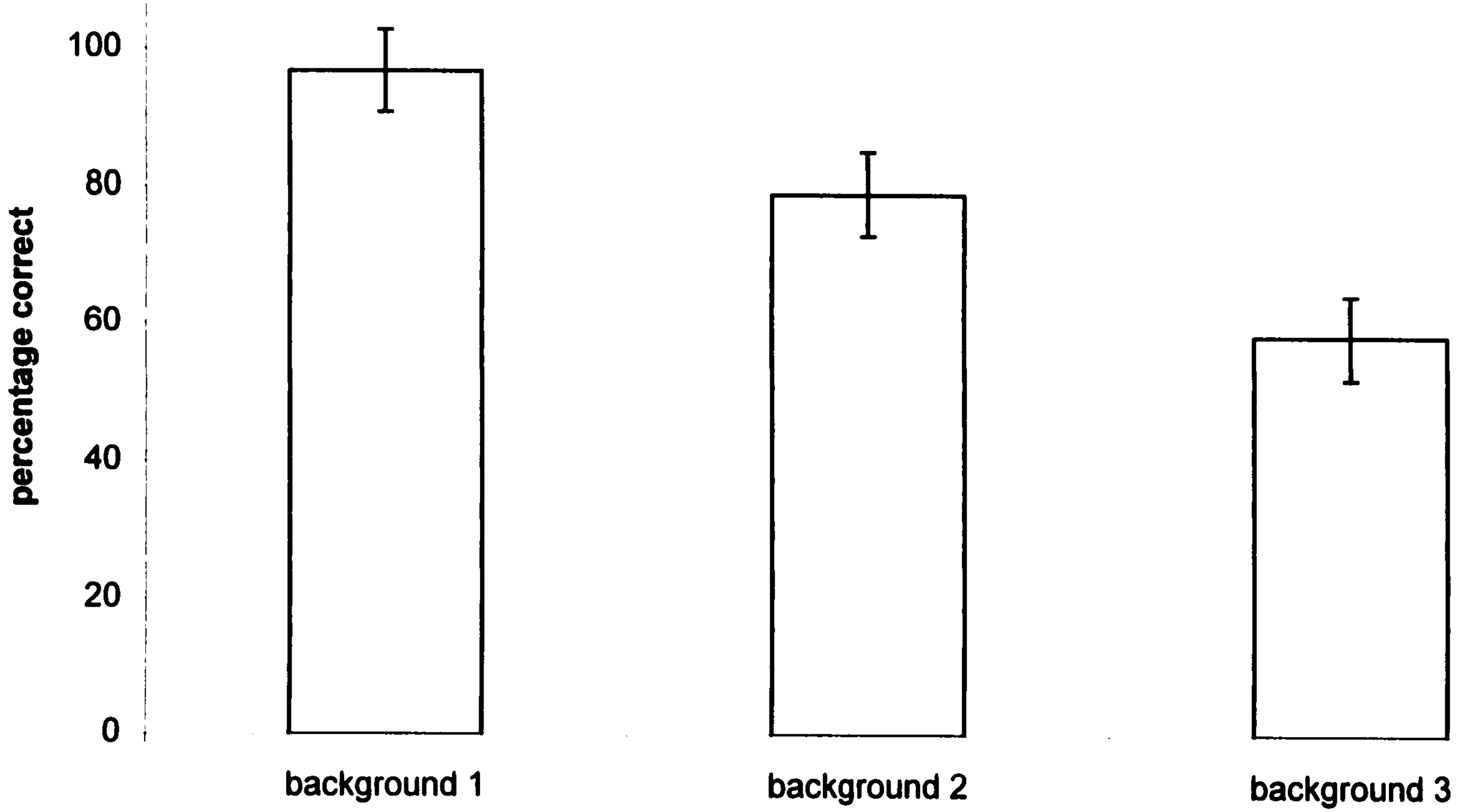


Figure 4G

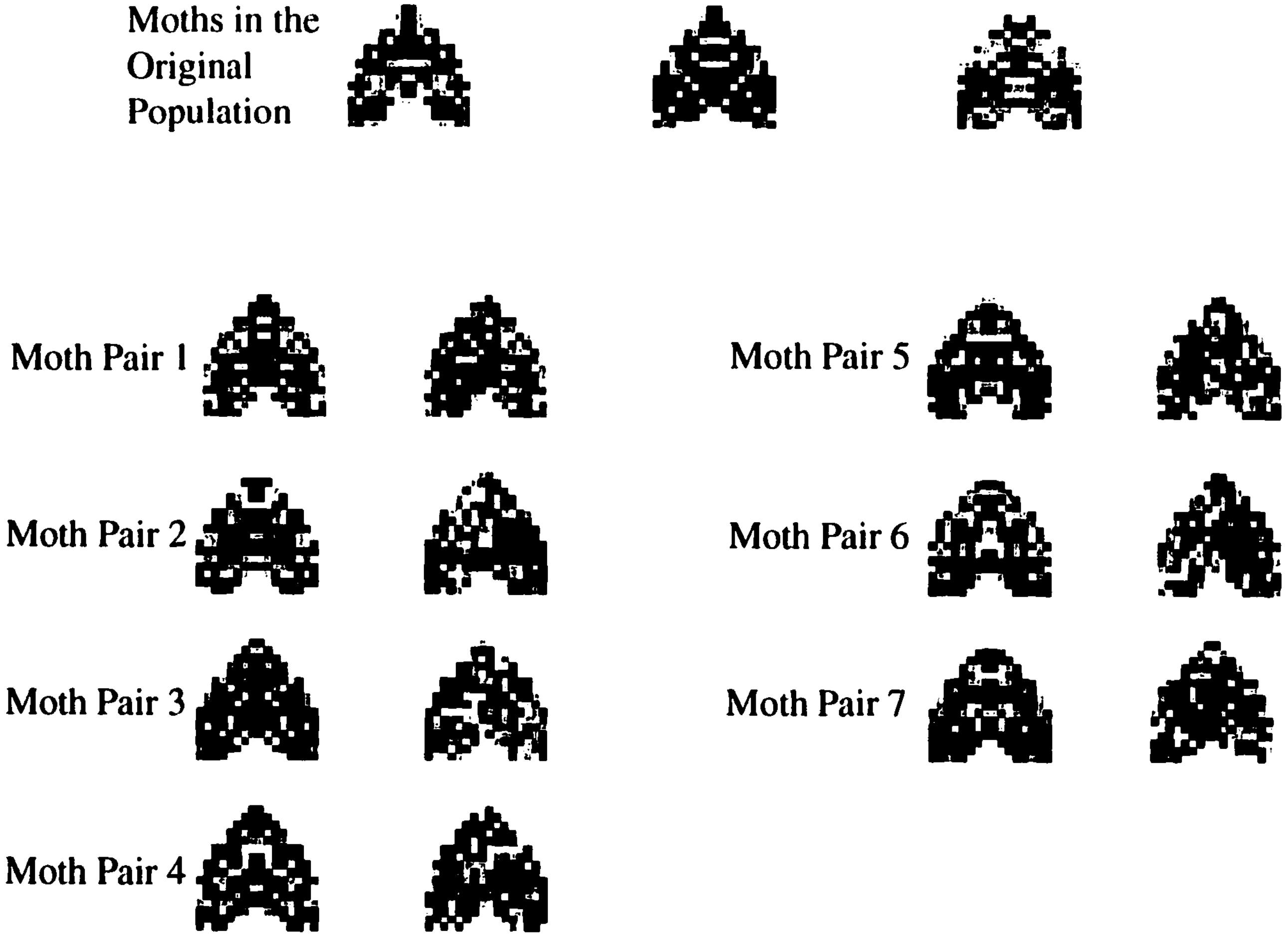

Moths in the Original Population
Moth Pair 1
Moth Pair 2
Moth Pair 3
Moth Pair 4
Moth Pair 5
Moth Pair 6
Moth Pair 7

Figure 4H

Replication 1

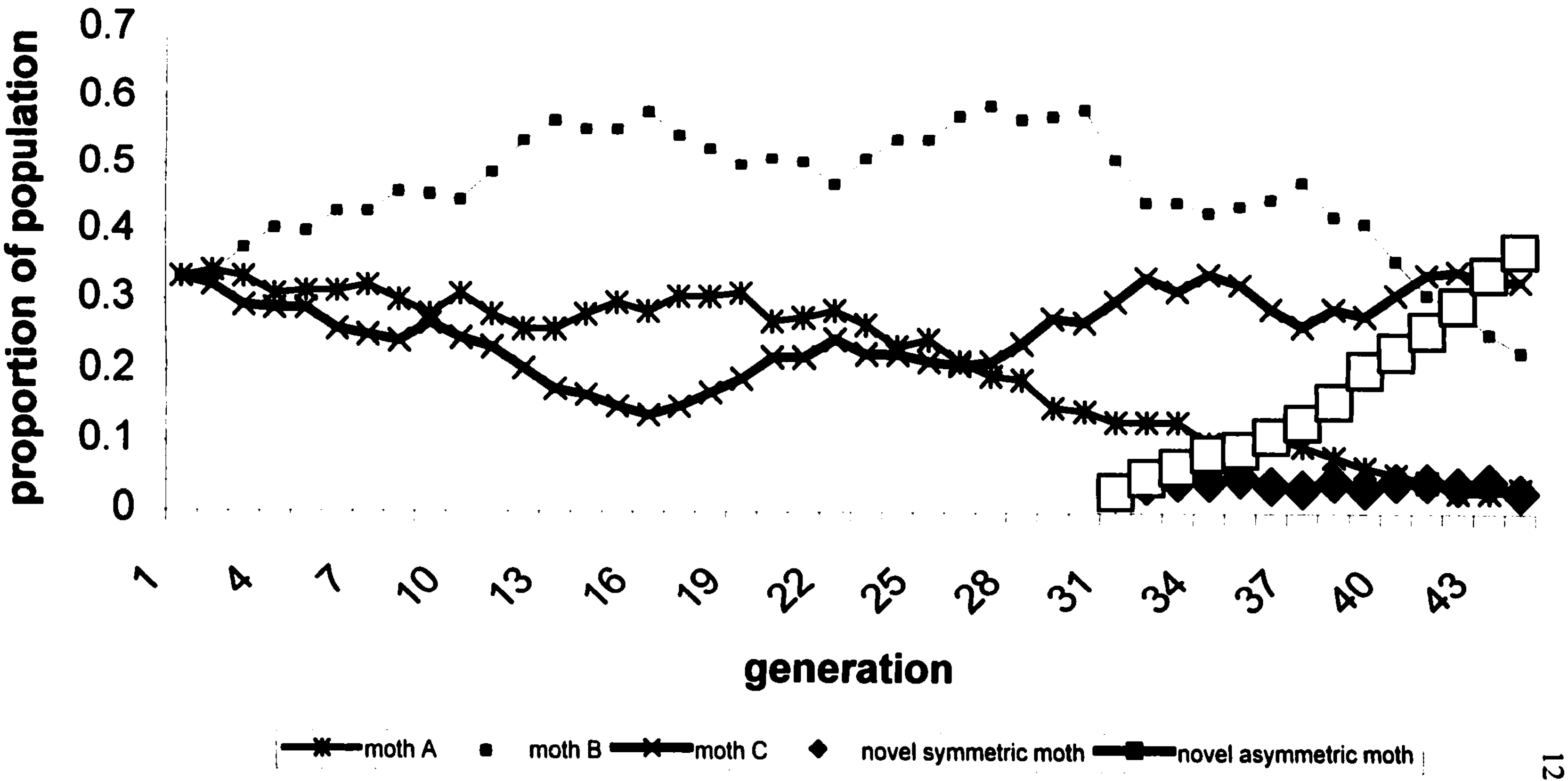
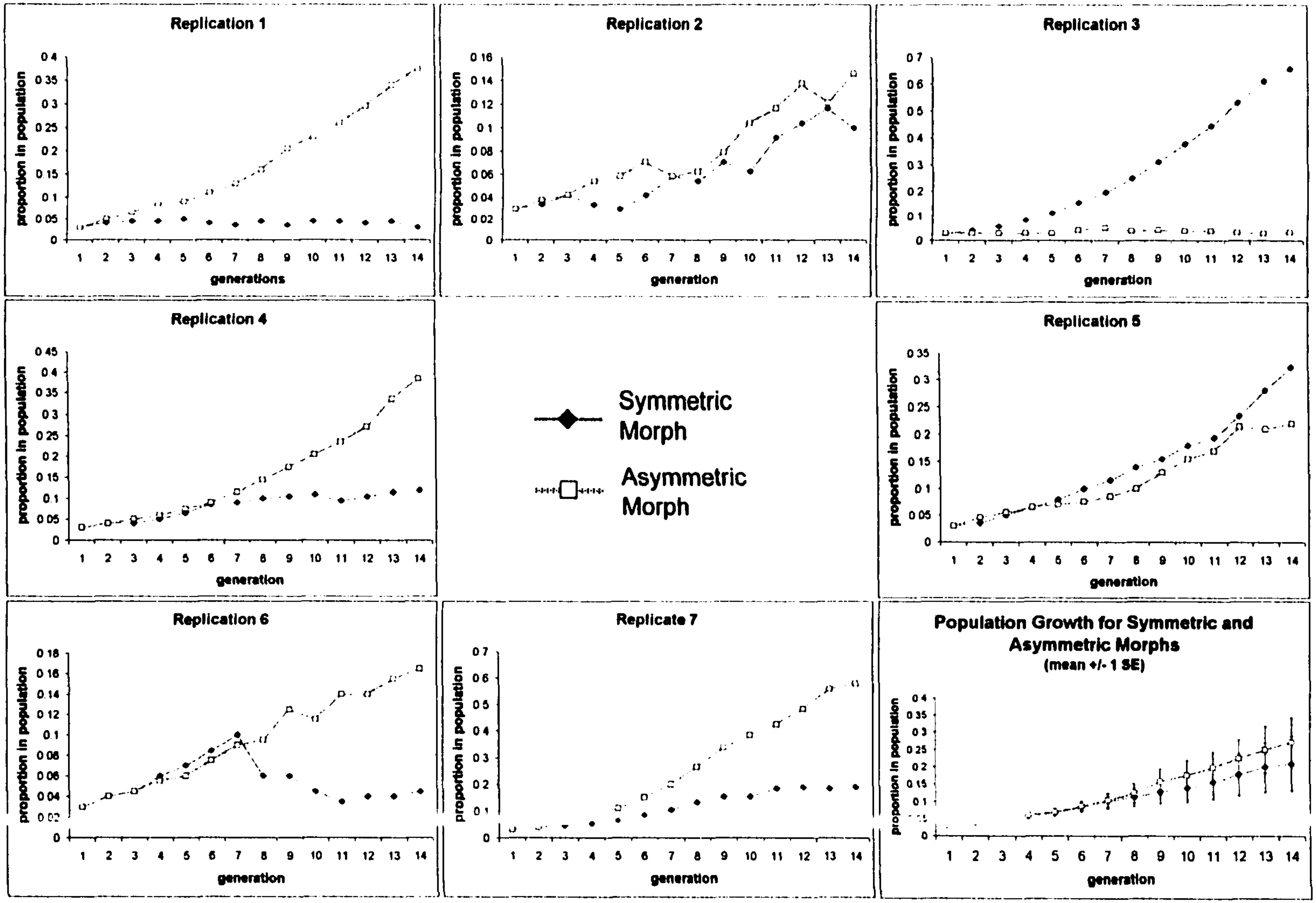


Figure 4I


Replication 1
proportion in population
generations
Replication 2
proportion in population
generation
Replication 3
proportion in population
generation
Replication 4
proportion in population
generation
Symmetric Morph
Asymmetric Morph
Replication 5
proportion in population
generation
Replication 6
proportion in population
generation
Replicate 7
proportion in population
generation
Population Growth for Symmetric and Asymmetric Morphs
(mean +/- 1 SE)
proportion in population
generation
1 2 3 4 5 6 7 8 9 10 11 12 13 14