

1-1-1977

Search image formation in the blue jay (*Cyanocitta cristata*).

Alexandra T. Pietrewicz
University of Massachusetts Amherst

Follow this and additional works at: https://scholarworks.umass.edu/dissertations_1

Recommended Citation

Pietrewicz, Alexandra T., "Search image formation in the blue jay (*Cyanocitta cristata*)."
(1977). *Doctoral Dissertations 1896 - February 2014*. 1488.
<https://doi.org/10.7275/n20h-tq10> https://scholarworks.umass.edu/dissertations_1/1488

This Open Access Dissertation is brought to you for free and open access by ScholarWorks@UMass Amherst. It has been accepted for inclusion in Doctoral Dissertations 1896 - February 2014 by an authorized administrator of ScholarWorks@UMass Amherst. For more information, please contact scholarworks@library.umass.edu.

SEARCH IMAGE FORMATION
IN THE BLUE JAY
(CYANOCITTA CRISTATA)

301

A Dissertation Presented
by
Alexandra T. Pietrewicz

Submitted to the Graduate School of the
University of Massachusetts in partial fulfillment
of the requirements for the degree of

DOCTOR OF PHILOSOPHY

August 1977

Psychology

SEARCH IMAGE FORMATION
IN THE BLUE JAY
(CYANOCITTA CRISTATA)

A Dissertation Presented
By
Alexandra T. Pietrewicz

Approved as to style and content by:

Alan C. Kamil

Alan C. Kamil, Chairperson of Committee

John W. Donahoe

John W. Donahoe, Member

Melinda A. Novak

Melinda A. Novak, Member

Theodore D. Sargent

Theodore D. Sargent, Member

Bonnie Strickland

Bonnie Strickland, Chairperson
Department of Psychology

Acknowledgements

I wish to thank my advisor, Dr. Alan C. Kamil, for his guidance, assistance, and inspiration during the course of this research and throughout my graduate career. I would also like to extend a note of thanks to my committee members, Dr. Melinda A. Novak, Dr. John W. Donahoe, and Dr. Theodore D. Sargent for their constructive comments and suggestions. I am especially grateful to John E. Mauldin for his encouragement and understanding throughout the course of this study and all my other professional endeavors. I would like to extend a very special note of appreciation to my parents, Edward S. and Alexandra E. Pietrewicz, not only for their unfailing support and enthusiasm for my work, but also for their friendship.

ABSTRACT

Search Image Formation
in the Blue Jay
(Cyanocitta cristata)

August, 1977

Alexandra T. Pietrewicz, B.S., M.S.,
Ph.D., University of Massachusetts

Directed by: Dr. Alan C. Kamil

Search image formation in the blue jay (Cyanocitta cristata) was investigated using operant discrimination procedures. A series of four experiments were conducted to test Tinbergen's (1960) search image hypothesis, which predicts that if a predator encounters the same prey type several times in a row, his ability to accurately detect that prey type should increase. The subjects were five blue jays (Cyanocitta cristata), previously trained to respond to the presence or absence of Catocala moths in photographs. Search image formation was tested here by presenting, within a discrimination session, a series of slides to the birds within which the positive (containing a moth) slides all contained the same Catocala species. Such a series was called a run, and performance during runs was compared with performance during non-runs, in which two different prey species were intermixed. Experiments 1 and 2 investigated this problem with run lengths of 16 positive (moth) slides intermixed with 16 matched negative (no moth) slides imbedded within testing sessions. There were four types of slide series in these two studies: CRYPTIC RUNS, in which all positive slides contained the same species of moth under cryptic conditions; NON-CRYPTIC RUNS, all positive slides contained the same species of moth under non-cryptic conditions; CRYPTIC NON-RUNS, in which positive

slides contained either of two species of moths under cryptic conditions; and NON-CRYPTIC NON-RUNS, in which positive slides contained either of two species of moths under non-cryptic conditions. In Experiment 1, slides of two Catocala species which are cryptic on the same background were used, and in Experiment 2, two species which are cryptic on different backgrounds were used. The results of Experiment 1 did not provide evidence of search image formation. However, the results of Experiment 2 showed that the jays detected cryptic moths better when presented with runs of one prey type than with non-runs of two species. This effect did not occur when the moths were presented in non-cryptic conditions. Although there was no systematic increase in ability to detect the cryptic moths with consecutive encounters with one prey type, the absence of such an effect may have been due to satiation with long session lengths. Experiments 3 and 4 tested search image formation with the same general procedures but with shorter run and non-run lengths, and with the moths appearing only under cryptic conditions. In these two experiments, there were three types of slide series imbedded within the discrimination sessions: RUNS of either of two Catocala species or NON-RUNS of the two species intermixed. These series were composed of 8 positive slides intermixed with 8 matched negative slides. In Experiment 3, slides of two Catocala species which are cryptic on different backgrounds were used, and in Experiment 4, the two moth species used were cryptic on the same background. The results of these experiments showed that the jays formed a search image when presented with runs of one prey type, as reflected by an increased ability to detect the cryptic moths with consecutive encounters with one prey type. In addition, the jays showed an increased ability to detect the absence of the moths in negative

slides, concurrently with the formation of a search image. When the non-run was composed of intermixing two moth species which are cryptic on different backgrounds, there was no evidence of search image formation. In addition, this non-run condition produced lower levels of detection accuracy than the run conditions. These results provide a direct demonstration of search image formation, as defined by a change in the ability to detect cryptic, familiar prey following a few consecutive encounters with that prey type. In addition, these results provide evidence for the development of an increased ability to detect the absence of a prey item during formation of a search image for that time.

Table of Contents

Abstract.....	iii
Acknowledgements.....	vi
List of Figures.....	ix
Introduction.....	1
Operant procedures and the assessment of search image formation.....	8
Method-General.....	12
Subjects.....	12
Apparatus.....	12
Procedure.....	14
Experiment 1.....	15
Method.....	16
Results.....	18
Discussion.....	29
Experiment 2.....	31
Method.....	32
Results.....	32
Discussion.....	40
Experiment 3.....	43
Method.....	44
Results.....	46
Discussion.....	51
Experiment 4.....	54
Method.....	55
Results.....	55
Discussion.....	59
General Discussion.....	61
Characteristics of search image formation.....	62
Specificity of the search image.....	65
Effects of polymorphism upon the detection of cryptic prey.....	66

Table of Contents (Continued)

References.....	68
Appendix A.....	70
Appendix B.....	89

List of Figures

Figure	Page
1 Mean percentage correct on positive slides within experimental blocks as a function of the position of the slides within each of the four experimental conditions (Experiment 1).....	21
2 Mean percentage correct on positive slides within the experimental blocks as a function of the distance from which the slides were taken. (Experiment 1).....	22
3 Mean response speed on positive slides in the experimental blocks as a function of crypticity in the slides and the position of the slides in the experimental blocks. (Experiment 1)....	24
4 Mean response speed on positive trials within experimental blocks as a function of experimental condition, distance, and position of the slides in the experimental blocks. (Experiment 1).....	25
5 Mean percentage correct on negative slides as a function of the distance from which the slides were taken and the position of the slides in the experimental blocks. (Experiment 1).....	27
6 Mean response speed to negative slides in the experimental blocks as a function of the background in the slide and the distance from which the slides were taken. (Experiment 1)....	28
7 Mean percentage correct on positive slides as a function of the position of the slides in the experimental blocks within each of the four experimental conditions. (Experiment 2).....	33
8 Mean percentage correct on positive slides as a function of the position of the slides in the experimental blocks and the distance from which the slides were taken. (Experiment 2).....	35

List of Figures (Continued)

Figure	Page
9	Mean percentage correct on positive slides as a function of crypticity, run type, and the distance from which the slides were taken. (Experiment 2)..... 36
10	Mean response speed to positive slides as a function of crypticity, distance from which the slides were taken, and position of the slides in the experimental block. (Experiment 2)..... 38
11	Mean percentage correct on negative slides as a function of run type, distance from which the slides were taken, and position of the slides in the experimental blocks. (Experiment 2)..... 41
12	Mean percentage correct on positive slides as a function of the condition within which the slides were presented, and the position of the slide in the experimental blocks. (Experiment 3)..... 47
13	Mean percentage correct on negative slides as a function of the condition within which the slides were presented and the position of the slides in the experimental blocks. (Experiment 3)..... 50
14	Mean percentage correct on positive slides as a function of condition of presentation and position of the slides in the experimental blocks. (Experiment 4)..... 57
15	Mean percentage correct on negative slides as a function of condition of presentation and position of the slides in the experimental blocks. (Experiment 4)..... 58

A large amount of research has been devoted to the analysis of predator-prey interactions and the response of predators to changes in the density of prey populations. Holling (1959) has called the relationship between rate of predation and the density of a prey species the functional response. He identified three types of functional response, the most interesting of which is the Type III functional response, exhibited by many vertebrates. This response is characterized by an S-shaped curve, reflecting the number of prey consumed as a function of increasing prey density. As prey density begins to increase, predators do not initially increase the number of prey captured. However, after some threshold density is reached, the number of prey taken rapidly increases. Finally, at high prey densities, the predator does not respond to further increases in density.

Many investigators have studied the behavioral mechanisms underlying the Type III functional response. One mechanism suggested to account for this functional response is the specific search image (Tinbergen, 1960). Tinbergen studied the hunting behavior of the Great Tit (Parus major) in a Scots pine forest in the Netherlands, by measuring the frequency of various species of prey in the tits' diet, most of which were cryptic, and the density of both predator and prey populations. Tinbergen tested the assumption that prey species at higher relative densities would be more heavily represented in the tits' diet than those at lower relative densities. His results, however, did not bear out this hypothesis. Rather, he found that certain species of prey were taken less frequently than predicted when the population density of that species was low. As the prey population became more dense, that prey species was captured much more frequently than expected, provided

the prey population had reached some critical threshold level. At high prey population densities, the prey were taken less frequently than expected. This Type III functional response could not be accounted for by fluctuations in density of other prey species, or by an increase in the size of the prey. Tinbergen suggested that the birds adopt a search image of the prey they are hunting when the prey population reaches some critical density.

Tinbergen suggested that search image involves the performance of a highly selective sieving operation on the visual stimuli reaching the retina (p. 332), although he did not attempt to speculate on the mechanism involved in this operation. Furthermore, he suggested that the adoption of a search image is a conditioning process which occurs soon after a new prey species occurs. The search image may be used in varying intensities, Tinbergen stated, and the intensity (or frequency) with which a search image is used depends upon the interaction of external factors such as size, conspicuousness, palatability, and prey density. At low prey densities, there are few chance encounters with that prey, and a search image for it would not be formed. As prey density increases, chance encounters with that prey increase, and the tit would form a search image. The formation of a search image would consequently allow for intense predation upon a single prey species. When the population reaches a high density, Tinbergen suggested that the birds abandon the search image for that prey in order to maintain a mixed diet, but this suggestion has been disputed (Gibb, 1952; Royama, 1970).

There have been investigations bearing on Tinbergen's search image hypothesis. However, many researchers have categorized different behavioral patterns as evidence of the use of search image by various predators, all of which

involve a differential response to different prey types. Some studies have shown that the predator focuses upon one prey species when other palatable prey are available at the same time. This pattern has been observed in the three-spined stickleback (Beukema, 1968) and in tits (Royama, 1970). Other studies have shown that a predator chooses one prey more frequently than another prey species, as in the wood pigeon (Murton, 1971), tits (Tinbergen, 1960), and Peromyscus (Holling, 1959). A few studies have demonstrated that some predators respond preferentially to a familiar prey object before responding to another, new prey (blackbirds, Alcock, 1973; trout, Ware, 1971; carrion crows, Croze, 1970), or that there is a time lag before a predator responds to newly introduced cryptic prey species, as in jays and chaffinches (deRuiter, 1952) and trout (Ware, 1971). Such indirect evidence has traditionally been assumed to support the hypothesis that many predators utilize a search image, or selectively choose a single prey species at a time, but the results of such studies do not require the assumption that these behavioral patterns in diverse species necessarily represent a common mechanism. Many of these results may be explained by prey preferences, differences in palatability of the prey, ease of capture or handling time, or avoidance of an unfamiliar food object (Krebs, 1973). Rather few studies, in fact, have investigated the adoption of a search image directly, where the behavior observed can be explained no other way, and factors such as prey preferences and differences in palatability are systematically controlled.

Croze (1970) conducted one of the few studies providing reasonable evidence of search image. He trained wild carrion crows to search for meat hidden under cryptic

shells on a beach, varying the model prey populations, their reinforcement value, and crypticity. He found that the crows quickly discovered a new food source and responded specifically to the visual characteristics of the shells. The crows required few encounters with a previously ignored camouflaged prey in order to detect it efficiently, and Croze assumed this result reflected a rapid formation of the search image. In addition, the crows did not respond to shells that differed from those for which they searched. Croze also found that the birds learned characteristics of the prey's location as well as visual characteristics of the prey, concentrating their search in the area where the prey were last found.

In a subsequent experiment, Croze attempted to determine whether visual polymorphism would increase survival rate of prey, using shell types with which the crows were familiar from the previous experiments. He first presented polymorphic (red, black, and yellow) populations of cryptic shells for three consecutive days. He then presented a monomorphic (all red, or black, or yellow) populations of cryptic shells on alternate days, and found that the crows responded to fewer shells in the polymorphic than in the monomorphic populations. However, the crows did not appear to choose shells in runs of one type in the polymorphic population. Croze assumed that the birds did not focus their search on one type of shell at a time in the polymorphic population, but instead, looked for all three types simultaneously. This suggestion is supported by the finding that the probability of the crows finding one type of shell in the polymorphic population was not dependent upon the type of monomorphic population presented on the previous day. The overall higher capture rate in the monomorphic populations is consistent with the search image hypothesis because detection was better when the crows were

searching for one prey type than for three prey types. Thus, the formation of a search image can account for the differences in detection between the monomorphic and polymorphic populations.

The finding that the crows did not take shells in runs of one type in the polymorphic population appears contradictory to the search image hypothesis. Croze reasoned that perhaps the crows did not encounter any one shell type with a high enough frequency to allow the formation of a search image. This explanation appears reasonable in view of the fact that the shell types in the polymorphic population were presented in equal numbers. Therefore, the density of any one prey type may have been lower than the critical threshold density necessary for the adoption of a specific search image. In addition, the fact that the polymorphic population was novel to the birds, although the individual prey types were familiar, may also have suppressed the formation of a search image. Although these studies provide little information on the conditions necessary for the adoption of a search image, they suggest that the crow uses a search image under at least some circumstances.

On the basis of his results, Croze postulated the following characteristics of search image: 1) there is a restriction of the releasing stimulus configuration and includes the visual properties of both the prey and its background; 2) search image may be the consequence of a few encounters and also involves changing the path of search; 3) search image includes either a complete exclusion of other stimuli, or not responding to other stimuli although they are perceived; and 4) search image is maintained by reward and shifts quickly with change in reward association. Croze conceded that the predator may, in fact, perceive

other stimulus configurations, but does not respond to them. Tinbergen, on the other hand, assumed that the search image is a sieving of the visual stimuli reaching the retina. Croze's data, however, suggests a learning of the prey's habitat in conjunction with adoption of a search image, although Tinbergen's data does not.

Dawkins (1971 a) emphasized the need for a more precise definition of search image, and suggested that situations where the predator's behavior can be explained only by a change in what the predator perceives should be considered as evidence of search image. This restriction would eliminate a number of behaviors as the cause of an observed change in searching behavior. In some situations, change in search may be due to the predator's altering his path of search as the result of learning where to hunt, a strategy demonstrated by Alcock (1973) and Croze (1970). A predator may also not eat a prey object the first time it is encountered due to a failure to attack, kill, or handle the prey efficiently. It would be necessary to determine if an increase in the number of a particular prey species captured is due to an improvement in motor patterns of handling. Dawkins further argued that a predator may focus on a preferred prey species, or may not accept a newly introduced species simply because it is novel. Such preference has been found by Croze (1970) and Allen and Clark (1968). Dawkins stated that only those changes in behavior shown when the predator is faced with cryptic, familiar food can be used as evidence for changes in the ability of the predator to perceive its prey.

On the basis of this argument, Dawkins (1971 a) conducted a study to determine the extent to which young chicks undergo changes in their ability to detect cryptic food, while feeding on green or orange grains of rice

scattered on green or orange stones. She found that chicks rarely took cryptic grains at the beginning of test sessions. However, once they had taken a few cryptic grains, they quickly began to take them much more frequently. Dawkins assumed this result was due to a difficulty in detecting cryptic grains early in testing, and that the increase in rate of finding cryptic grains later in testing was due to the chicks' learning to detect them. Subsequent tests showed that the birds did not retain an ability to find cryptic rice from one day to the next, and that feeding on conspicuous grains actually decreased the chicks' ability to detect cryptic food. Although she concluded that chicks undergo changes in ability to detect cryptic food, her conclusions are questionable because none of the chicks had experience with cryptic grains before the start of testing. Thus, her procedure does not meet her own requirement that changes in searching behavior can be considered as evidence of search image only when a predator is faced with cryptic familiar food. It cannot be determined whether the increase in the number of cryptic grains taken was due to some perceptual change or to an increased familiarity with a novel, cryptic food source.

In a subsequent study, Dawkins (1971 b) investigated the possibility that chicks switch attention to different stimulus cues when feeding on cryptic and conspicuous grains of rice. She hypothesized that chicks feeding on cryptic grains attend to non-color cues, such as size and shape, and that chicks feeding on conspicuous grains attend to color cues. She attempted to test this hypothesis by manipulating types of grain upon which the chicks fed prior to testing with a choice between familiar color grains and different color cryptic grains. Her results, however, were inconclusive, and she was unable to determine

the cues to which the chicks attended.

Although Dawkins failed to determine the cues to which the chicks attended, she did provide a specific testable definition of search image in terms of perceptual changes which result in an increased ability to detect cryptic, familiar prey following a few encounters with it. It is clear that past studies on search image have produced results which can be explained by the operation of factors other than this perceptual change. In view of these studies, it is evident that research in the area of searching strategies has lacked adequate experimental techniques which control for differences in prey preferences, palatability, handling time, and avoidance of novel prey. However, a methodology has recently been developed directly from techniques of operant conditioning and discrimination learning, which allows control of these factors and will be used in the present study to analyze the conditions necessary for the formation of a specific search image.

Operant procedures and the assessment of search image formation

Pietrewicz (1975) and Pietrewicz and Kamil (1977) used a technique for the study of detection of cryptic prey by blue jays (Cyanocitta cristata), similar to procedures used by Herrnstein and Loveland (1964) and Siegel and Honig (1970), in studies of concept formation in pigeons. Essentially, the procedure involved standard operant discrimination training using projected images as discriminative stimuli. The images were sets of slides taken in the laboratory or in the field, some of which contained a moth, and some of which contained no moth. Blue jays were trained to differentially respond to the presence or absence of moths in the slides, projected upon a large pecking

key. The birds were exposed to a large set of slides in which Catocala moths appeared on a matching or non-matching bark substrate, or on an artificial, non-bark substrate. The slides were prepared in matched pairs; for each positive slide (containing a moth), there was a matched negative slide (containing no moth), identical except for the absence of the moth. Positive slides included an equal number of each of three Catocala species: C. resecta, which has grey-brown forewings with a disruptive pattern of grey and brown lines, and rests head-down on trees such as oak and maple; C. cara, which has brown forewings with faint disruptive markings of brown lines and rests in caves, under eaves, or head-down on dark tree trunks; and C. relictata, which has white forewings with patches and stripes of black and grey running horizontal to the body axis, and rests head-up on trunks of white birch trees.

Pietrewicz tested the ability of the jays to detect these moths in slides as a function of the moths' substrate, orientation on the substrate, and distance from which the photographs were taken. It was expected that, if the photographs of moths were reasonable models of natural prey, the ability of the jays to detect the moths would depend upon those factors assumed to affect the detection of these prey in the wild. Sargent (1966; 1968; 1969) and Sargent and Keiper (1969) have identified two aspects of the behavior of Catocala which probably affect their crypticity. These moths select resting substrates which match the reflectance of their forewings and adopt species-typical body orientations on the substrate, which align their disruptive markings with those of the substrate. Thus, matching substrate and appropriate orientation of the moths in the slides might be expected to decrease the ability of the jays to detect the moths. In addition, in-

creased distance from which the slides were taken should produce poorer detection when the moths were cryptic than when conspicuous. Croze (1970) found that the distance from which prey were detected was shorter for well-camouflaged prey than for conspicuous prey.

In the slide sets used, each species occurred equally often on each of three substrates (oak, birch, and non-bark), in each of three orientations (head-up, head-down, and horizontal), and at each of five subject to camera distances (2, 4, 8, 12, 16 feet). The birds were trained on the discrimination problem in the following manner. Each trial began with illumination of a small, round, change-over (CO) key with red light. If the jay pecked the CO key once, a slide was projected from the rear upon a large stimulus key, and the CO key changed to illumination by a white cross on a black background. If the projected slide was positive, 10 pecks at the stimulus key resulted in the delivery of reinforcement (half of a meal-worm), followed by an intertrial interval (ITI) of 10 seconds to allow ingestion of reinforcement. Pecks at the CO key during positive trials were followed by a 60 second ITI. In the presence of negative slides, a peck at the CO key terminated the trial, and after a 4 second ITI, the next trial was begun. If 10 pecks were made to the stimulus key during a negative trial, the 10th peck was followed by a 60 second ITI.

The results of this study reflected several major effects. The jays successfully learned the discrimination problem, responding at 75-90% correct on both positive and negative slides. The use of matched pairs of positive and negative slides assured that this level of performance reflected the birds' responding to the moths and not to some other visual components of the slides. Furthermore,

crypticity and orientation of the moths had dramatic effects upon the jays' ability to detect the moths. Accuracy of detection was poorest when the moths presented on their matching backgrounds, while detection was extremely accurate when the moths were presented on a non-matching substrate. When the moths were presented on matching substrates, horizontal orientation produced better detection than vertical orientations in which disruptive marking were aligned with markings of the bark. In general, accuracy of detection decreased with increased distance from which the slides were taken, but increased distance produced the greatest reduction in detection when the moths were placed on a matching substrate. These effects of crypticity, orientation, and distance of the moths were reflected not only in accuracy of detection, but also in speed of responding to the slides. The conditions which produced least accurate detection produced the slowest response speeds.

Since these results indicate that detection of simulated prey is affected by factors which probably operate in the wild, these procedures represent an excellent technique for the study of specific search image formation. Although this technique of studying blue jays hunting for a prey item normally preyed upon in the wild (Sargent, 1973) is artificial in some respects, it has a number of advantages for the study of search image. First, it is possible to control prey preferences, palatability, ease of capture and avoidance of unfamiliar prey, because with these procedures the jays do not eat the prey they detect. Chance encounters with a particular prey type can be simulated by controlling the sequence of slides presented. By imbedding a run of trials of a certain species of moth within a session, it should be possible to determine whether

there is an increased ability to detect cryptic moths following a few encounters. In addition, it should be possible to determine specifically those conditions under which this increased ability of detection occurs, by varying the length of the run and the crypticity of the moths. Finally, these techniques offer excellent measures of detection, in terms of both accuracy and speed, not possible under field or semi-natural conditions. In fact, these procedures allow such measures of detection under conditions of both the presence and absence of prey. The present research, then, was an investigation of search image formation using these operant conditioning procedures.

Method - General

Subjects. The subjects were 5 Northern blue jays (Cyanocitta cristata) obtained locally in the Amherst, Massachusetts area when approximately 10-12 days old, and hand-raised in the laboratory. The subjects ranged in age from 4 to 8 years old. All subjects received prior experience in learning set studies in a modified Wisconsin General Test Apparatus, and were trained to differentially respond to the presence or absence of moths in photographs. The subjects were maintained at 80% ad lib weight during the course of the experiment by controlled daily feeding.

Apparatus. The operant chamber was a Lehigh Valley Electronics cubicle, the subject chamber of which measured 33 x 30.5 x 35.5 cm. A food magazine was located centrally on one wall, and was illuminated whenever food was delivered. An 11.4 x 7.5 cm stimulus key was mounted to the left of the magazine, 12.7 cm above the floor. Slides

were projected upon this key from the rear, by a programmable Kodak Carousel 800 projector. On the right side of the magazine, a transparent (2.54 cm diameter) Lehigh Valley key (change-over key) was mounted 15.2 cm above the floor. An IEE multiple stimulus projector was mounted directly behind this key. Reinforcement consisted of halves of mealworms (Tenebrio larvae) and were delivered into the magazine by a Davis Universal feeder (Model UF-100) located on top of the operant chamber. A wooden perch was located 8.9 cm in front of the intelligence panel, 5.1 cm above the floor, so that the subjects' eye level fell roughly along the horizontal midline of the stimulus key. White noise was delivered through a speaker mounted on the front wall, and a ventilating fan at the rear of the chamber also provided masking noise. A houselight was mounted in the upper right corner of the intelligence panel and was illuminated during all experimental sessions. All stimulus presentations, contingencies, and data recording were controlled by a Lehigh Valley Electronics INTERACT system located in an adjacent room.

The stimulus slides used were taken from the set of slides used by Pietrewicz (1975). These slides were taken in a lightly wooded area between 10 a.m. and 4 p.m. Half the slides were positive, containing a moth in the resting posture, and half were identical negative slides without the moth. These slides were prepared in matched pairs by pinning a dead moth into position, taking a picture of the scene, then removing the moth and taking another picture. Three species of moths were used in the preparation of the slides: Catocala cara, C. retecta, and C. relictata. Each species was photographed from 5 distances (2, 4, 8, 12, and 16 feet), in three orientations (head-up, head-down, and horizontal), and on three substrates (oak, white birch, and

non-bark). C. cara normally rests in a head-down position and was most cryptic on the oak substrate; C. relictata normally rests in a head-up position and was most cryptic on white birch; C. retecta normally rests in a head-down position and was most cryptic on the oak substrate. Across all slides, the quadrant in which the moth appeared varied randomly. A more extensive description of these slides may be found in Pietrewicz (1975).

General Procedure. During all experiments in the present research, the following response requirements and reinforcement contingencies were used. Each trial began with illumination of the change-over (CO) key with red light. When the CO key was pecked once by a jay, a slide was projected upon the stimulus key, and the display on the CO key changed to illumination by a white cross on a black background. If the projected slide was positive (containing a moth), the bird was reinforced following 10 pecks at the stimulus key. Reinforcement was followed by a 10 second intertrial interval (ITI) to allow ingestion of the reward before the next trial began. A peck at the CO key on positive trials was followed by a 60 second ITI. On negative trials (slides containing no moths), a peck at the CO key terminated the trial and there was a 4 second ITI before the next trial began. On negative trials, the 10th peck at the stimulus key was followed by a 60 second ITI.

Experiment 1

The most basic prediction of Tinbergen's search image hypothesis seems to be that if a predator encounters the same prey type several times in a row, his ability to accurately detect that prey type should increase. This prediction can be tested with the current procedures by presenting a series of slides, within a session, within which the positive instances are all of the same Catocala species. Such a series is called a run, and performance during runs can be compared to performance during non-runs, in which 2 or more prey species are intermixed.

There were several expected results of this experiment. It was expected that when the slides were presented in runs of one cryptic species, there would be an increased accuracy of detection across trials of the runs. This result would suggest the formation of a search image, since search image is defined as an increased ability to detect cryptic prey after a few consecutive encounters with it. In addition, it was expected that this effect would occur for cryptic conditions only. Tinbergen (1960) assumed that a search image is formed only for cryptic prey. When a particular prey species is conspicuous against its substrate, detection is much more accurate than when the prey is cryptic (Pietrewicz, 1975), and thus, formation of a search image would not be used to increase the ability to detect the prey. Therefore, it was expected that under conspicuous conditions, there would be no increased ability to detect the moths across trials within the runs; conspicuous runs and conspicuous non-runs of the prey types should produce similar levels of performance in terms of accuracy of detection.

It was expected that overall levels of performance, in terms of accuracy of detection, should reflect better

detection of cryptic moths when the moths were presented in runs than when presented in non-runs, independent of an increase in detection across trials within the run. The RUN condition may be considered as equivalent to the presentation for a monomorphic population, since all positive slides within the run contained the same species of moth. The NON-RUN condition, on the other hand, may be considered as equivalent to presentation of a polymorphic population, since all positive slides contained either of two species of moth. Considering Croze's (1970) finding that crows captured more prey while hunting in monomorphic than in polymorphic populations, it was expected that blue jays would show better detection of cryptic moths while hunting in a simulated monomorphic population. This same effect was not expected under conditions where the moths were conspicuous, since conspicuous prey should be readily detected independent of the prey types presented on previous trials.

Method

A set of 128 slides was used in this experiment: 32 slides contained C. resecta, and 32 slides were matched negatives; 32 slides contained C. cara, with 32 matched negatives. Within this set of slides, each species occurred twice at each of 4 distances (4, 8, 12, and 16 feet), in each of two orientations (head-up and head-down), and on each of two substrates (oak and non-bark).

The jays were exposed to these slides, using the response requirements and reinforcement contingencies described above, in sessions of 68 trials, one session per day, over 16 days. Within each session, Trials 1-4 were warm-up trials, including 2 positive and 2 negative slides randomly chosen from the slide sets described by Pietrewicz (1975), with the stipulation that none of the

warm-up slides were contained in the set described above. Trials 5-36 were Experimental Block 1, and Trials 37-68 were Experimental Block 2. Within each block, there were 16 positive slides and 16 matched negative slides.

Each experimental block of trials within the session represented one of the following conditions: RUNS - the 16 positive slides all contained the same species of moth; NON-RUNS - 8 positive slides contained C. retecta, and 8 positive slides contained C. cara. In addition, runs and non-runs occurred either with all positive slides containing cryptic moths, or all positive slides containing non-cryptic moths. Thus, there were 4 major types of slide presentations in the experimental blocks: CRYPTIC RUNS (C. retecta or C. cara, on oak); CRYPTIC NON-RUNS (C. retecta and C. cara, on oak); NON-CRYPTIC RUNS (C. retecta or C. cara on the non-bark substrate); and NON-CRYPTIC NON-RUNS (C. retecta and C. cara on the non-bark substrate).

Each session of testing was designated a RUN session, or a NON-RUN session. In RUN sessions, one experimental block was a cryptic run, and the other experimental block was a non-cryptic run, each type occurring in the first and second experimental blocks equally often. In NON-RUN sessions, one experimental block was a cryptic non-run, the other a non-cryptic non-run, and each type occurred in the first and second experimental blocks equally often. The order of presentation of session types was random; over the 16-day testing period, there were 8 RUN sessions and 8 NON-RUN sessions, with a total of 16 experimental blocks of runs, and 16 experimental blocks of non-runs.

The order of presentation of slides within each experimental block of trials was counterbalanced in the following manner. Order of presentation of positive slides was random with the exception that each experimental block

began with a positive slide, and no more than 3 consecutive positive slides occurred. The positions of the 16 positive slides within the experimental block were designated Positions 1-16. Positive slides within each type of experimental block (e.g. CRYPTIC RUNS) were counterbalanced so that each distance (4, 8, 12, and 16 feet) occurred equally often in each of the 16 positions in the block. Orientation of the moths in positive slides (head-up or head-down) varied randomly. Negative slides were randomly intermixed with the positive slides, with the exception that no more than 3 consecutive negative slides occurred. The positions of the negative slides were counterbalanced so that each distance occurred equally often in each of the 16 negative slide positions. In addition, for both positive and negative slides within each block, each distance (4, 8, 12, and 16 feet) occurred once in Positions 1-4, 5-8, 9-12, and 13-16, in order to avoid a consecutive string of positive or negative slides of any particular distance.

Results

Since search image effects were expected on positive (containing a moth) trials, and the negative slides were included in the experimental blocks to control the overall density of "prey", performance on positive and negative slides was analyzed separately. The jays responded at a mean of 87.9% correct on positive trials, and at a mean of 84.2% correct on negative trials. These high levels of performance indicate that the birds successfully retained their ability to discriminate the presence and absence of moths in these slides from previous experiments.

The results of the analyses of variance (ANOVA) for this and subsequent experiments are presented in

Tables 1-16 of Appendix A.

Performance on positive trials of experimental blocks

ANOVA of percentage correct on positive trials revealed no significant differences in performance between RUN and NON-RUN conditions, under either cryptic or non-cryptic conditions. Under cryptic conditions, the jays responded at a mean of 82.5% correct on RUNS, and at 85.6% correct on NON-RUNS. Under non-cryptic conditions, the jays responded at a mean of 91.8% correct on both RUNS and NON-RUNS. Although overall performance on cryptic slides (84.1% correct) was lower than on non-cryptic slides (91.8% correct), this difference was not statistically significant, $F(1,4) = 6.99, p > .05$.

Although there was no significant main effect of position of the slide in the experimental block upon percentage correct, the jays' performance did vary as a function of position within the four experimental conditions. Figure 1 presents percentage correct on positive slides as a function of position of the slides within each of the four experimental conditions. There was an increase in percentage correct across positions 1-12 in the CRYPTIC RUN and both NON-CRYPTIC conditions, but a subsequent decrease in performance in positions 13-16 under these conditions. In the CRYPTIC NON-RUN condition, there was a continuous decrease in percentage correct across positions. This differential effect across position for cryptic and non-cryptic conditions was reflected in a significant Run type X Crypticity X Position interaction, $F(3, 12) = 5.10, p < .025$.

Figure 2 presents percentage correct on positive slides as a function of distance within the four experimental conditions. There was no general decrease in percentage correct with increased distance from which the

slides were taken, as found by Pietrewicz (1975). There was a slight decrease in percentage correct with increased distance, up to 12 feet, for both cryptic and non-cryptic RUN conditions. In the cryptic NON-RUN condition, there was a large decrease in percentage correct between slides taken at 4 feet and slides taken at 8 feet, and a small increase at 12 feet. The non-cryptic NON-RUN condition resulted in small increases in percentage correct at 8 and 12 feet. The differential effects of distance as a function of crypticity and run type resulted in a significant Run type X Crypticity X Distance interaction, $F(3, 12) = 6.20$, $p < .01$, although there was no main effect of distance, $F(3, 12) = 2.99$, $p > .05$.

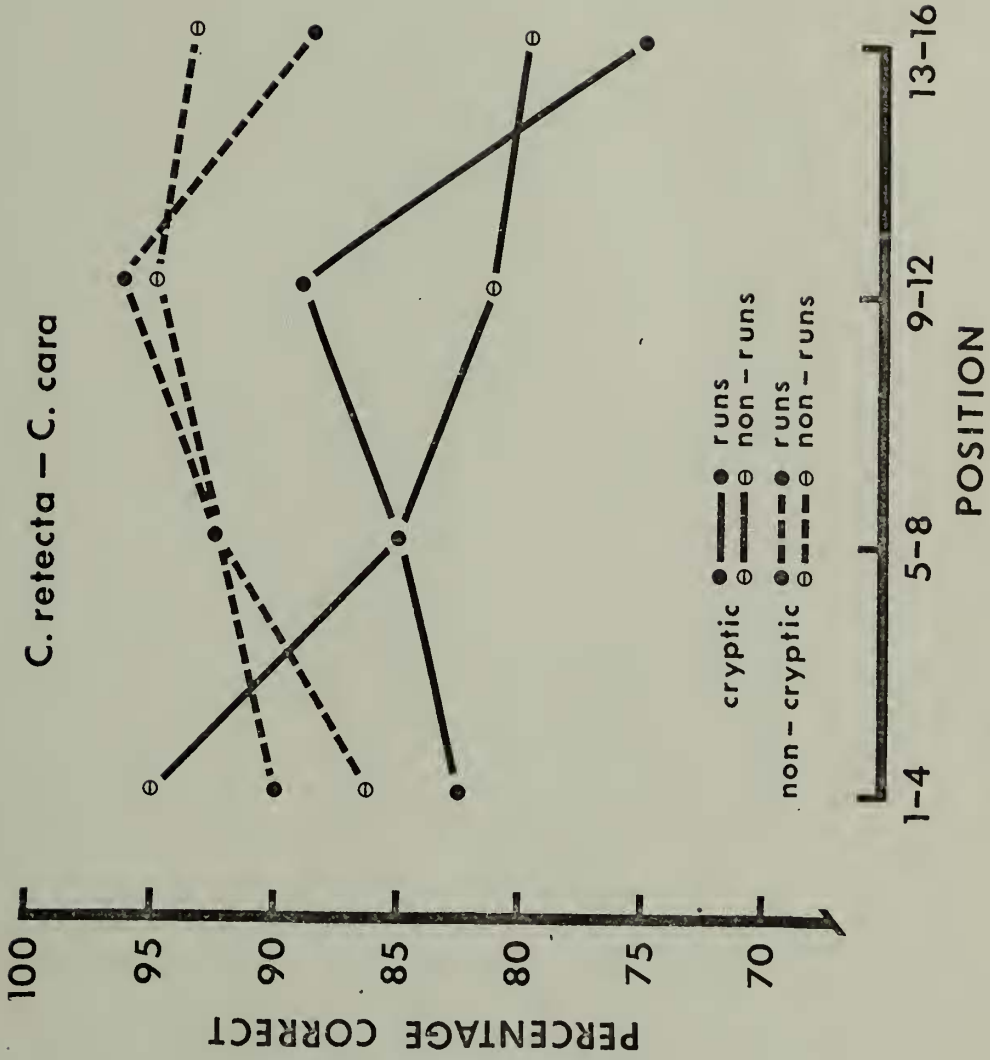
Performance on positive slides was also analyzed in terms of response speed (reciprocal of latency, in seconds, between a peck at the CO key, starting a trial, and the first response to the slide or CO key). It was expected that factors affecting accuracy of detection of the moths would similarly affect the speed of responding to the slides. However, the results were not consistent with this prediction. There was a significant effect of position of the positive slides in the experimental blocks upon response speed, $F(3, 12) = 6.46$, $p < .01$, but this effect was represented by a decrease in response speed across position. The jays responded at a mean speed of .434 to slides in positions 1-4; at .426 for positions 5-8; at .406 for positions 9-12; and at .332 for positions 13-16. In addition, this decrease in response speed across position was greater on cryptic slides than on non-cryptic slides, resulting in a significant Crypticity X Position interaction, $F(3, 12) = 5.37$, $p < .025$. The effects of these variables upon response speed are shown in Figure 3.

The analysis of response speed on positive trials also resulted in significant interactions of Run type X

FACE PAGE FOR FIGURE 1

Figure 1. Mean percentage correct on positive slides within experimental blocks as a function of the position of the slides within each of the four experimental conditions. (Experiment 1).

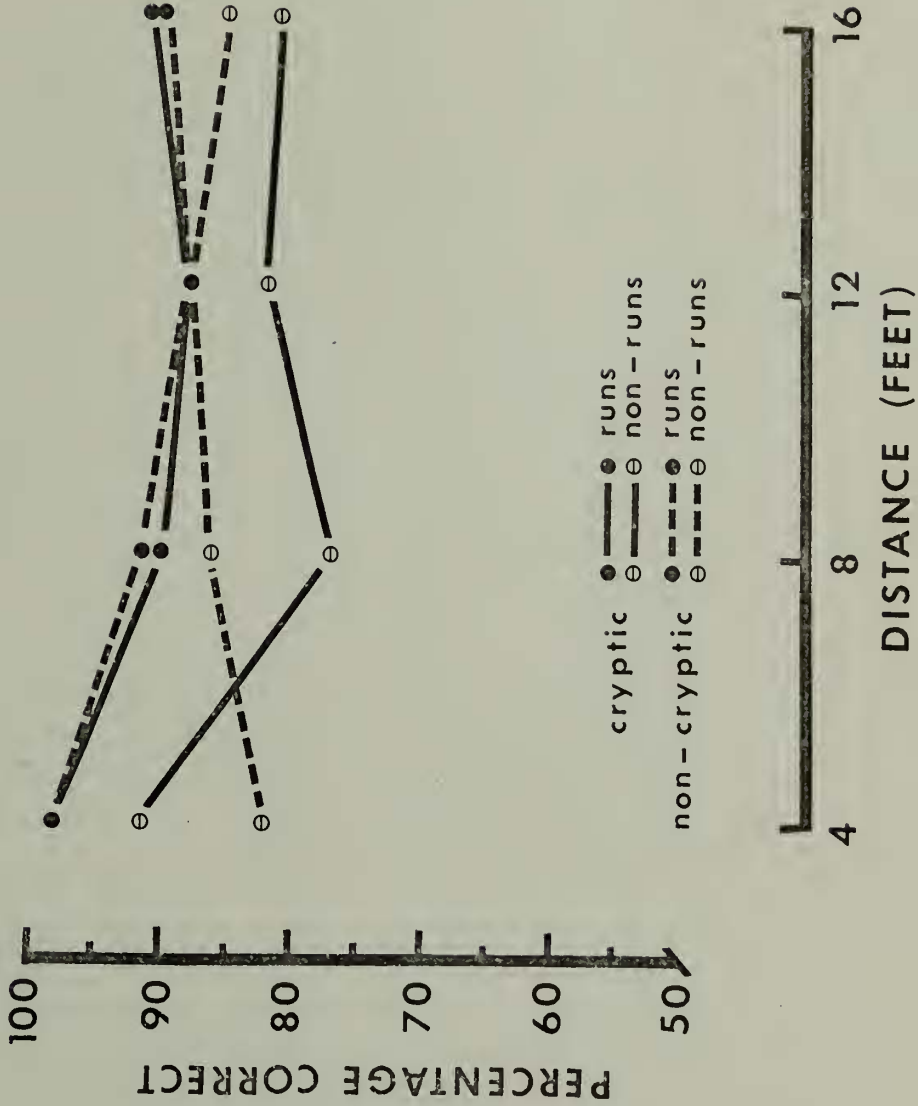
C. resecta - C. cara



FACE PAGE FOR FIGURE 2

Figure 2. Mean percentage correct on positive slides within the experimental blocks as a function of the distance from which the slides were taken. (Experiment 1)

C. relecta — *C. cara*



Crypticity X Position, $F(3,12) = 3.68$, $p < .05$, and Run type X Crypticity X Position X Distance, $F(9,36) = 4.98$, $p < .001$. Figure 4 presents response speed as a function of the four experimental conditions, distance, and position of the slides in the experimental blocks. These factors produced highly variable effects upon response speed. The RUN conditions resulted in the most dramatic overall decreases in response speed across position, but within each of these conditions, the shape of the function differed for each distance. In both RUN conditions, response speed to slides taken at 4 feet was slower than to slides taken at 8, 12, and 16 feet, a result which is not consistent with the results of Pietrewicz (1975). The NON-RUN conditions produced slightly less variable effects upon response speed, but again, there were no consistent trends across position or distance.

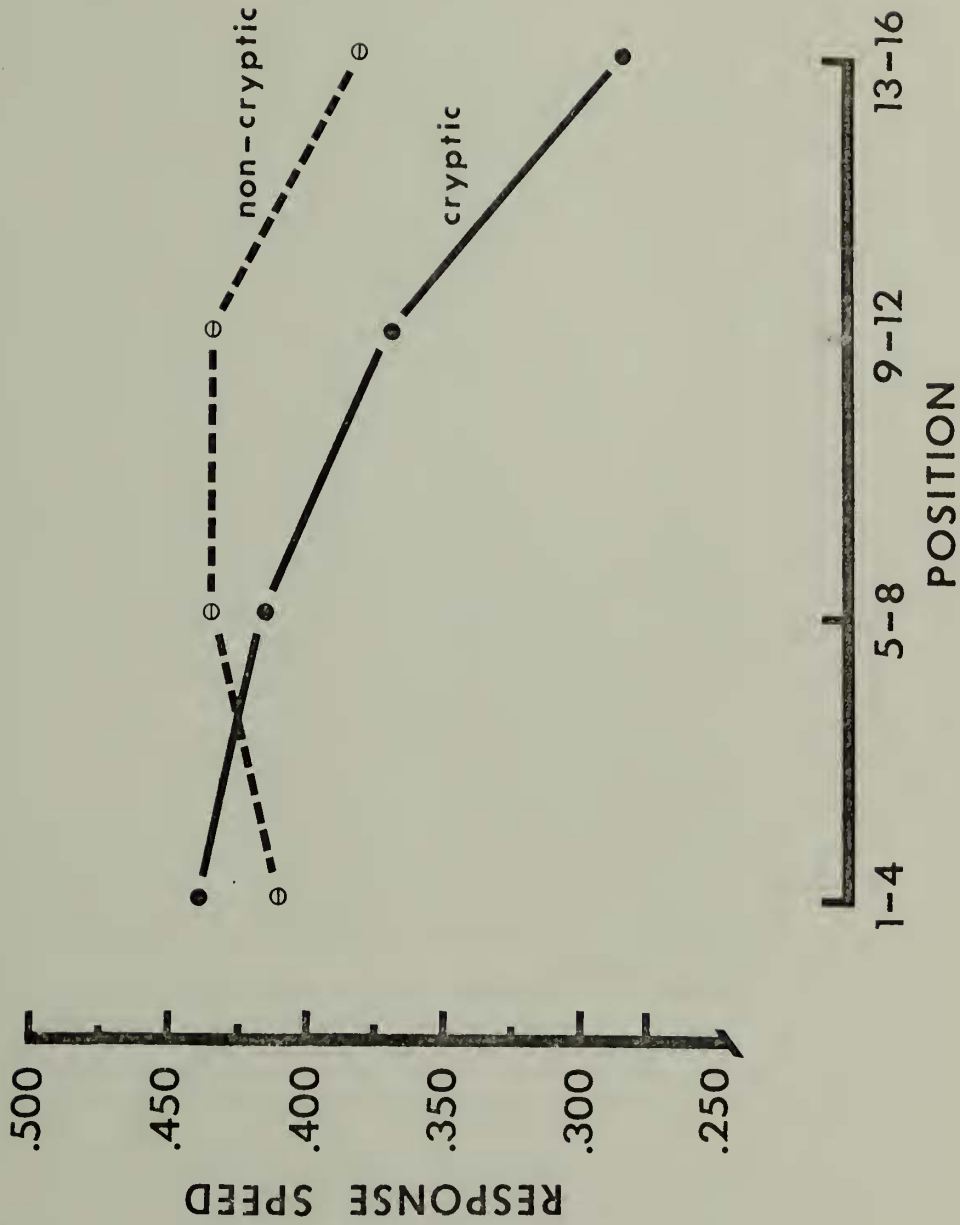
Performance on negative trials of experimental blocks

ANOVA of percentage correct on negative trials revealed no significant difference in performance between RUNS and NON-RUNS. Subjects responded to negative slides at 83.1% correct during RUNS, and at 85.3% correct during NON-RUNS. In addition, performance on negative slides did not differ significantly between slides containing oak substrates (intermixed with cryptic positives) and slides containing the non-bark background (intermixed with non-cryptic positives). The jays responded at a mean of 81.2% correct to negatives containing oak, and at a mean of 87.1% correct to negatives containing the non-bark background.

Although there was no effect upon percentage correct of presenting negative slides in RUNS or NON-RUNS, the position of the negative slide in the experimental block

FACE PAGE FOR FIGURE 3

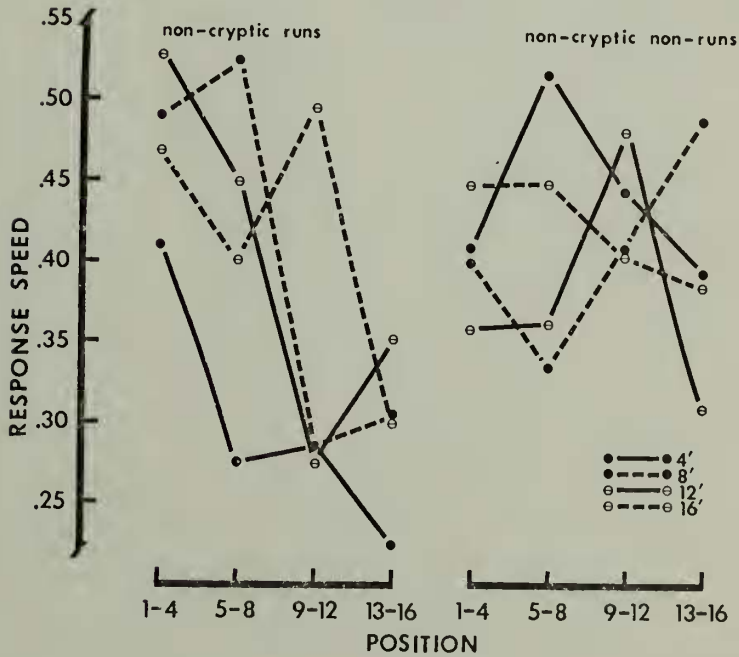
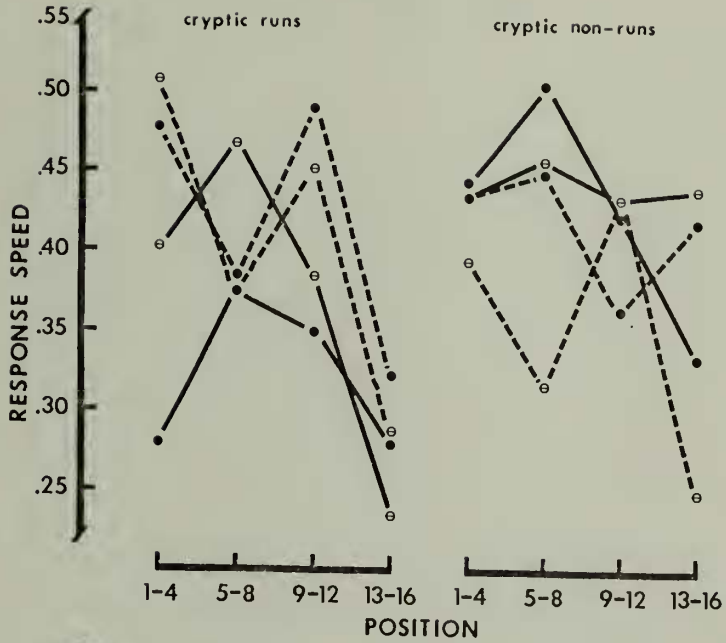
Figure 3. Mean response speed on positive slides in the experimental blocks as a function of crypticity in the slides and the position of the slides in the experimental blocks. (Experiment 1)



FACE PAGE FOR FIGURE 4

Figure 4. Mean response speed on positive trials within experimental blocks as a function of experimental condition, distance, and position of the slides in the experimental blocks. (Experiment 1).

C. RETECTA - C. CARA

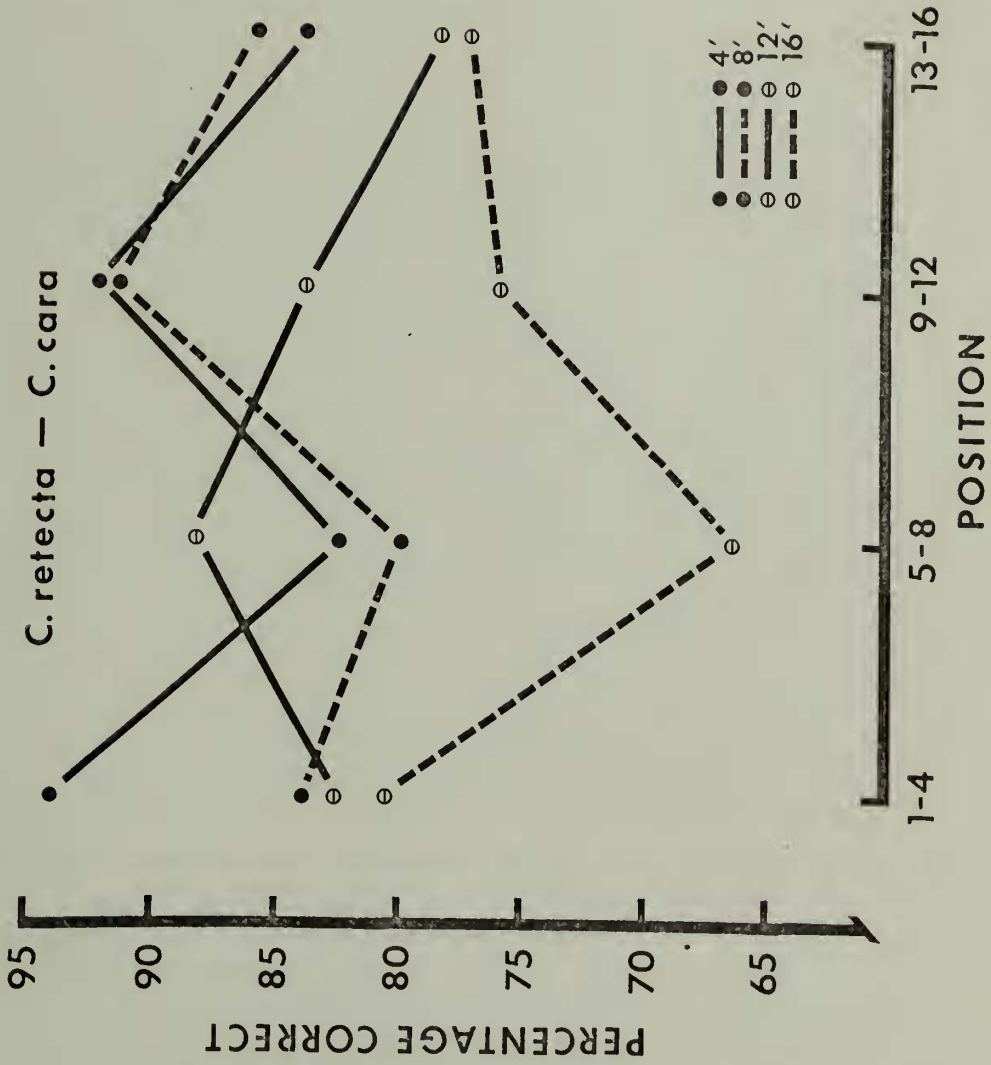


had a significant effect upon percentage correct performance, $F(3,12) = 6.98$, $p < .01$. The jays responded at a mean of 88.4% correct to slides in positions 1-4, at 79.9% correct in positions 5-8, at 86.7% correct in positions 9-12, and at 81.9% correct in positions 13-16. In addition, the effect of position on percentage correct varied with the distance from which the negative slide was taken. Figure 5 presents percentage correct performance on negative slides as a function of position and distance. On negative slides taken at 4, 8, and 16 feet, there was a decrease in percentage correct between positions 1-4 and positions 5-8, and an increase between positions 5-8 and positions 9-12. On negative slides taken at 12 feet, there was an increase in percentage correct between positions 1-4, and 5-8, and subsequent decreases in performance at 12 and 16 feet. These differential effects of position as a function of distance upon performance resulted in a significant Distance X Position interaction, $F(9,36) = 2.22$, $p < .05$.

Positions of the negative slides in the experimental blocks also affected response speed to the slides as well as percentage correct. The jays responded to negative slides at a mean speed of .213 in positions 1-4 and positions 5-8, at .198 in positions 9-12, and at .174 in positions 13-16. This decrease in response speed across position was significant, $F(3,12) = 6.16$, $p < .01$. In addition, the effect upon response speed of distance from which the negative slides were taken varied significantly as a function of the type of background in the slide, $F(3,12) = 8.2$, $p < .005$. Figure 6 presents mean response speed as a function of background and distance in the negative slides. Mean response speed to negative slides containing oak background was slowest at distances of 14

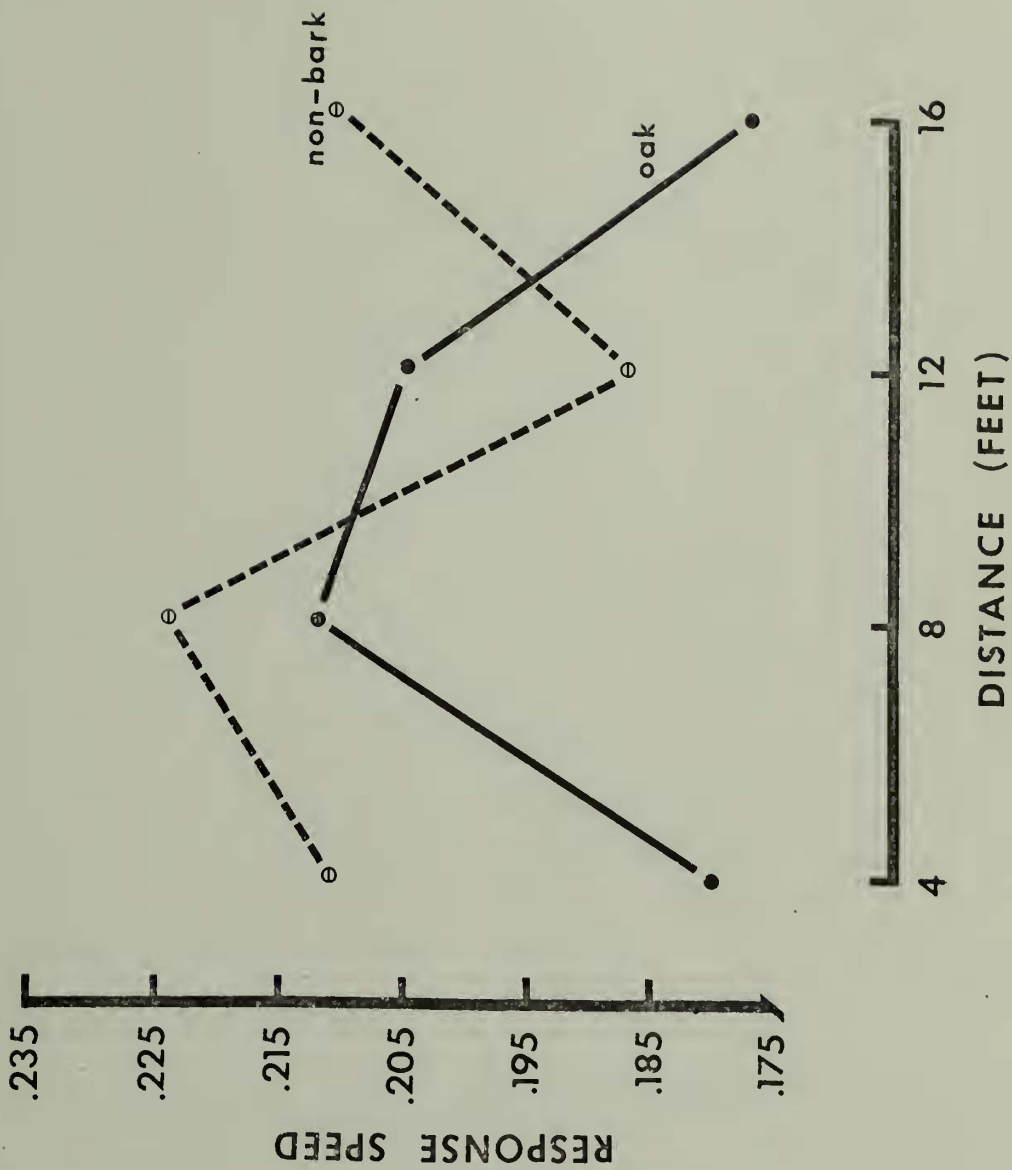
FACE PAGE FOR FIGURE 5

Figure 5. Mean percentage correct on negative slides as a function of the distance from which the slides were taken and the position of the slides in the experimental blocks. (Experiment 1)



FACE PAGE FOR FIGURE 6

Figure 6. Mean response speed to negative slides in the experimental blocks as a function of the background in the slide and the distance from which the slides were taken. (Experiment 1)



and 16 feet, while the mean response speed to negative slides containing the non-bark background was slowest at 12 feet. The jays responded faster to negative slides containing the non-bark background (mean = .206) than to those containing the oak background (mean = .194); however, this difference in response speed was not statistically significant, $F(1,4) = 1.45, p > .05$.

Discussion

Two important findings are evident in these results. First, the jays did not form a specific search image when presented with consecutive encounters with one cryptic species. Second, the jays did not detect the moths more readily when runs of one cryptic species were presented than when both cryptic species were presented during non-runs. Although there was some increase in accuracy of detection across the first 12 positive trials of CRYPTIC RUNS, the subsequent decrease in accuracy of detection in positions 13-16 suggests that a search image was not utilized.

The fact that the jays did not show better detection of the moths in CRYPTIC RUNS than in CRYPTIC NON-RUNS is consistent with Croze's (1970) finding that cryptic prey are detected more readily in simulated monomorphic populations than in simulated polymorphic populations. However, the similarity in appearance between C. cara and C. retecta, and the fact that these species were both presented on the same background in the cryptic condition, may have minimized the difference between CRYPTIC RUNS and CRYPTIC NON-RUNS in the current experiment.

Croze (1970), in his investigation of the effects of mono- and polymorphism upon rate of predation, used three highly cryptic, but differently colored, shells: red-yellow (red and grey base, blue, burnt umber and yellow

powder colors added), yellow (pale grey base, with yellow, burnt sienna and black powder colors added), and black (white base, with black and burnt amber powder colors added). Because these shell types differed greatly in coloration, they were probably quite different visually to the crows. Croze was able to achieve a cryptic appearance with these differently colored shells because the background upon which they were placed was itself variable, a large beach shingle littered with pebbles. The simulated polymorphism in the present study, on the other hand, consisted of two species, relatively similar in coloration, placed on similar trunks of oak trees. The similarity in appearance of the two species, the fact that the area searched (oak trunks) was much smaller than that in Croze's study, and the consistency of the background from trial to trial (as compared to Croze's pebbled, uneven background) may have operated to produce more similarity between the RUN and NON-RUN conditions than was present in Croze's study.

The absence of an increase in accuracy of detection across positive trials of CRYPTIC RUNS should be considered in view of two aspects of the procedures used. First, the orientation of the moths varied within RUN conditions, head-up and head-down occurring equally often. This variation in the stimulus configuration of the cryptic moths within the run may have precluded search image formation. These data suggest that consistency of the stimulus configuration may be a necessary condition for search image formation.

The second aspect of the procedures which should be considered is the length of the test sessions. The fact that percentage correct on both positive and negative trials decreased over positions 13-16, in addition to the fact that response speed decreased in these positions, suggests

that overall performance may have decreased by the end of the test session. In fact, the jays had never before been tested in sessions as long as 68 trials. The slight increase in percentage correct in positions 1-12 of CRYPTIC RUNS suggests that search image may have begun to develop, but the long session length may have reduced any tendency to maintain high levels of detection accuracy.

The next experiment was designed to test search image formation under the same experimental conditions but using two species of moths which were very different visually.

Experiment 2

This experiment was a replication of the first experiment, except that the species of moth presented were visually dissimilar, and appeared cryptic on different backgrounds: C. resecta, an oak mimic, and C. relictata, a birch mimic. The use of two very differently colored species and substrates could result in effects upon detection more similar to those obtained in Croze's simulated polymorphic populations.

Croze (1970) stated that search image is not only a restriction of the releasing stimulus situation, but also includes visual properties of both the prey and its background, involving a response based upon knowledge of the prey's location, in addition to filtering of irrelevant stimuli. In this experiment, cryptic conditions consisted of presentations of C. relictata on birch, and C. resecta on oak so that the type of bark presented predicted the species of moth which was potentially present. Therefore, the consistency of presentation of only one moth species on one type of bark substrate could facilitate search image formation. Such a finding would support the hypothesis that visual components of the substrate are part of the search image.

Method

Experiment 2 was conducted in exactly the same manner as Experiment 1, except that a corresponding set of slides of C. relictata, cryptic on birch, was substituted for the set of slides of C. cara, which is cryptic on oak.

Results

The jays responded at a mean of 82.9% correct on positive trials, and at a mean of 81.1% correct on negative trials, maintaining their previous high levels of performance. As in the first experiment, performance on positive and negative trials in the experimental blocks was analyzed separately.

Performance on positive trials of experimental blocks

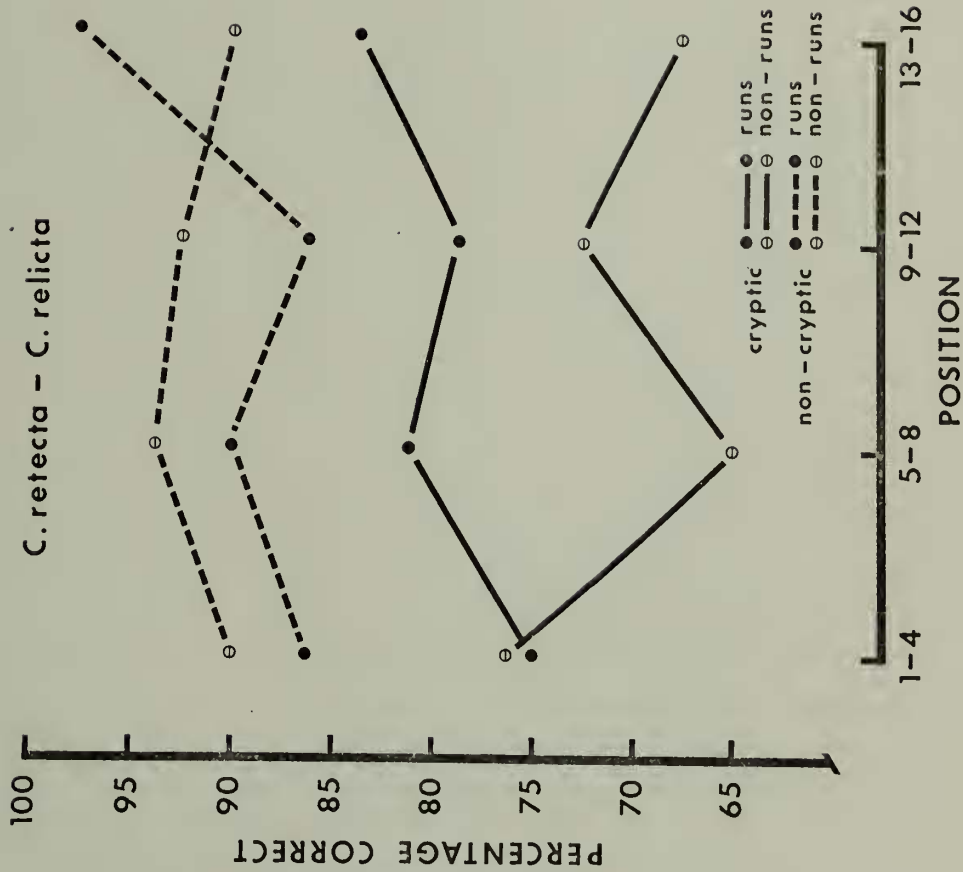
ANOVA of percentage correct on positive trials revealed that under cryptic conditions, the jays detected the moths more accurately in RUNS than in NON-RUNS. The jays responded at a mean of 79.7% correct on CRYPTIC RUNS, and at a mean of 70.3% correct on CRYPTIC NON-RUNS. Under non-cryptic conditions, performance was similar on RUNS and NON-RUNS. The jays responded at a mean of 90.0% correct on NON-CRYPTIC RUNS, and at a mean of 91.6% correct on NON-CRYPTIC NON-RUNS. These differential effects of crypticity and run type upon percentage correct resulted in a significant Run type X Crypticity interaction, $F(1,4) = 19.6$, $p < .025$.

Figure 7 presents percentage correct on positive slides as a function of the position of the slide in the experimental blocks. The jays responded at a mean of 81.9% correct on slides in Positions 1-4, at 82.5% correct on slides in Positions 5-8 and 9-12, and at 84.7% correct on slides in Positions 13-16. Within the CRYPTIC RUN conditions, there was also some increase in percentage correct across position of the slide in the run. The jays

FACE PAGE FOR FIGURE 7

Figure 7. Mean percentage correct on positive slides as a function of the position of the slides in the experimental blocks within each of the four experimental conditions. (Experiment 2)

C. relecta - C. relecta



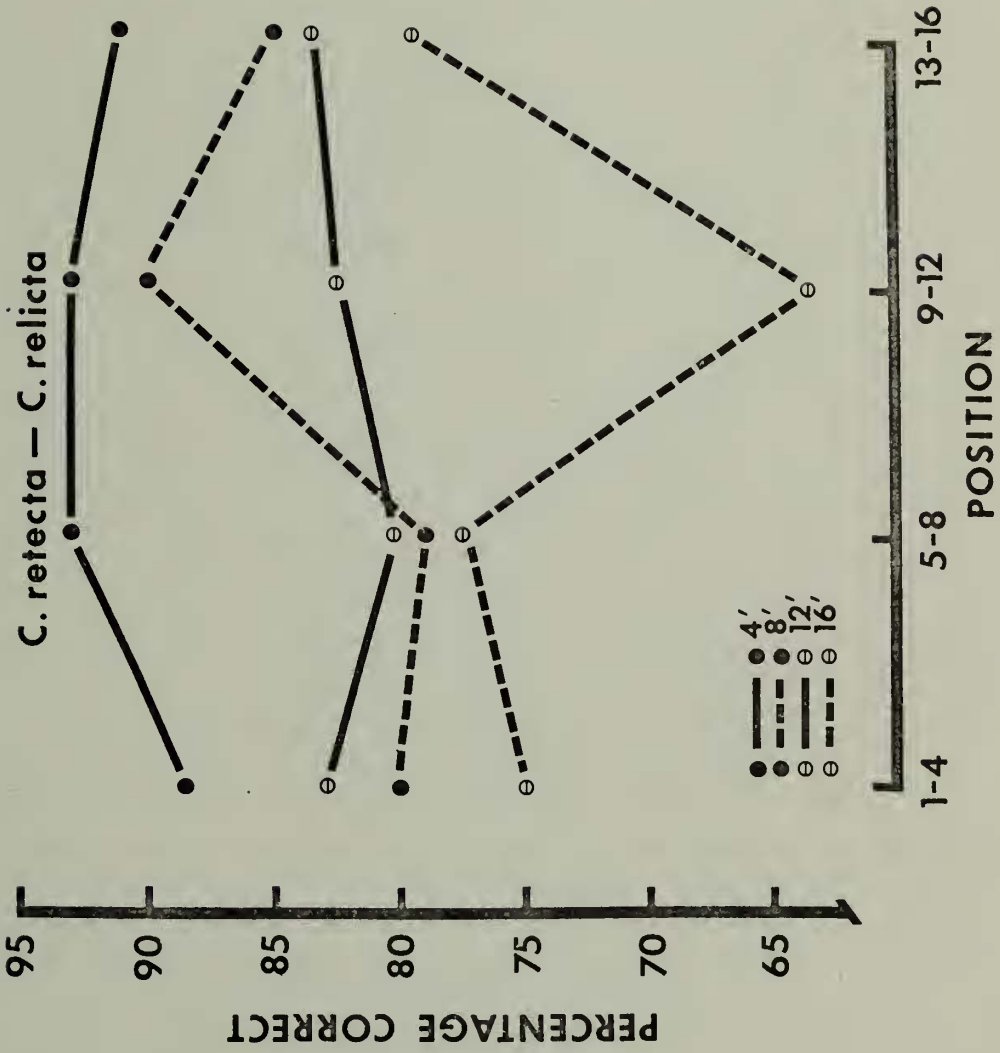
responded to positive slides in this condition at a mean of 75.0% correct in positions 1-4, at 81.3% correct in positions 5-8, at 78.8% correct in positions 9-12, and at 83.8% correct in positions 13-16. However, these increases in percentage correct across position were not statistically significant.

The effect of the position of the slides in the experimental blocks was found to vary with the distance from which the slides were taken. Figure 8 presents percentage correct on positive slides as a function of position of the slides and the distance from which the slides were taken. There was a general decrease in percentage correct with increased distance, $F(3,12) = 7.80, p < .005$. In addition, percentage correct at each distance varied with the position of the slide. Performance on slides taken at 4 feet remained relatively stable across position. Performance on slides taken at 8 and 12 feet decreased between positions 1-4 and 5-8, and increased between positions 5-8 and 9-12. On slides taken at 16 feet, percentage correct increased between positions 1-4 and 5-8, decreased at positions 9-12, and increased at positions 13-16. This variation in percentage correct as a function of both distance and position resulted in a significant interaction of these factors, $F(9,36) = 3.08, p < .025$.

Figure 9 presents percentage correct on positive slides as a function of distance from which the slides were taken within the four experimental conditions. Under non-cryptic conditions, there was a gradual decrease in percentage correct with increased distance from which the slides were taken. In the CRYPTIC RUN condition, there was a more dramatic decrease in performance with increased distance. The CRYPTIC NON-RUN condition produced the most variable performance with increased distance; percentage

FACE PAGE FOR FIGURE 8

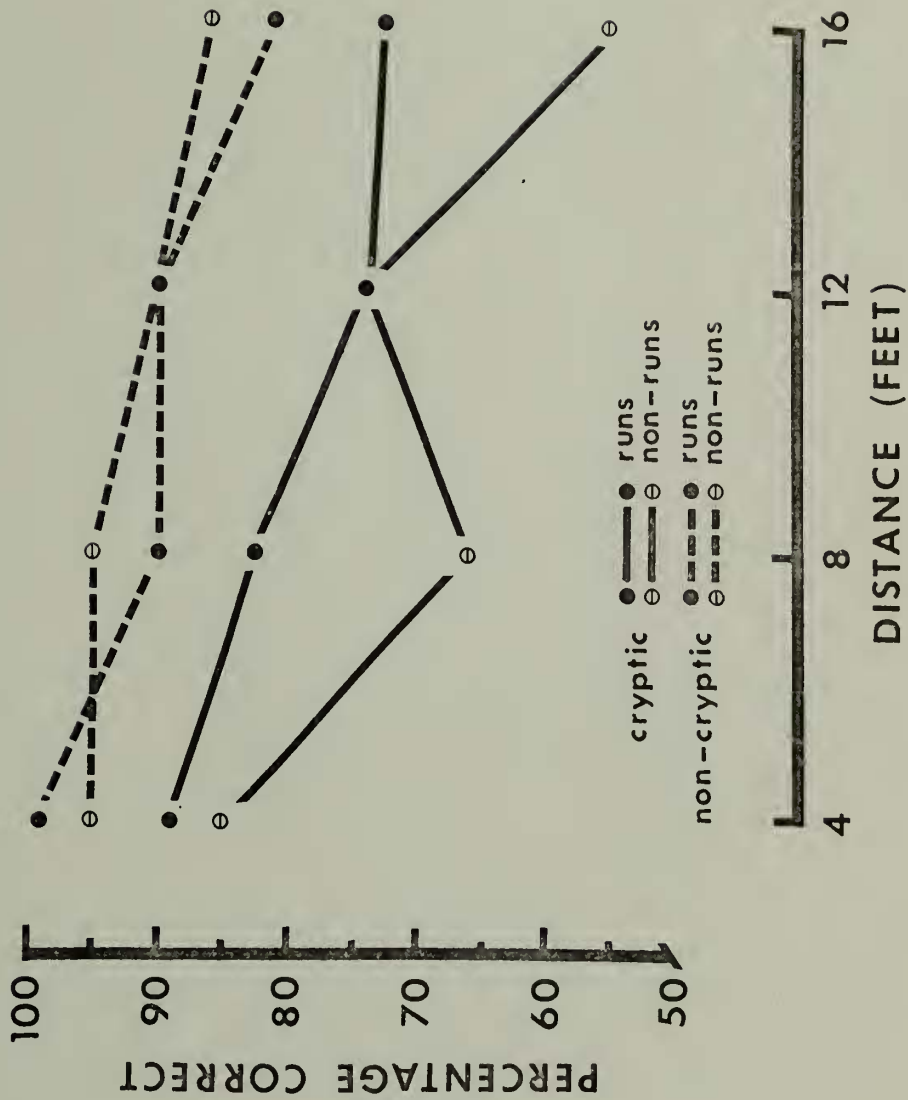
Figure 8. Mean percentage correct on positive slides as a function of the position of the slides in the experimental blocks and the distance from which the slides were taken. (Experiment 2)



FACE PAGE FOR FIGURE 9

Figure 9. Mean percentage correct on positive slides as a function of crypticity, run type, and the distance from which the slides were taken. (Experiment 2)

C. relecta - *C. relecta*



correct decreased on slides taken at 8 feet, increased at 12 feet, and decreased again at 16 feet. This differential effect of distance upon percentage correct as a function of the experimental condition resulted in a significant Run type X Crypticity X Distance interaction, $F(3,12) = 10.27, p < .005$.

Response speed to positive slides was generally slower under cryptic conditions (mean = .349) than under non-cryptic conditions (mean = .413). In addition, the effects of the position of the slide upon response speed varied as a function of distance from which the slides were taken. Figure 10 presents mean response speed as a function of crypticity, distance, and position of the slides. There was no consistent trend of increasing or decreasing response speed across position as a function of distance, in either the cryptic or non-cryptic conditions. Under cryptic conditions, the jays showed a decrease in response speed to slides taken at 4 feet, across position, but response speed to slides taken at 8, 12, and 16 feet was highly variable across position. Under non-cryptic conditions, the jays responded to slides taken at 12 feet with increased response speed across positions 1-12, but there was no consistent change in response speed across position to slides taken at 4, 8, or 16 feet. Because each distance produced characteristically different curves of response speed as a function of position of the slide, there was a significant Crypticity X Distance X Position interaction, $F(9,36) = 3.19, p < .01$.

Performance on negative trials of experimental blocks

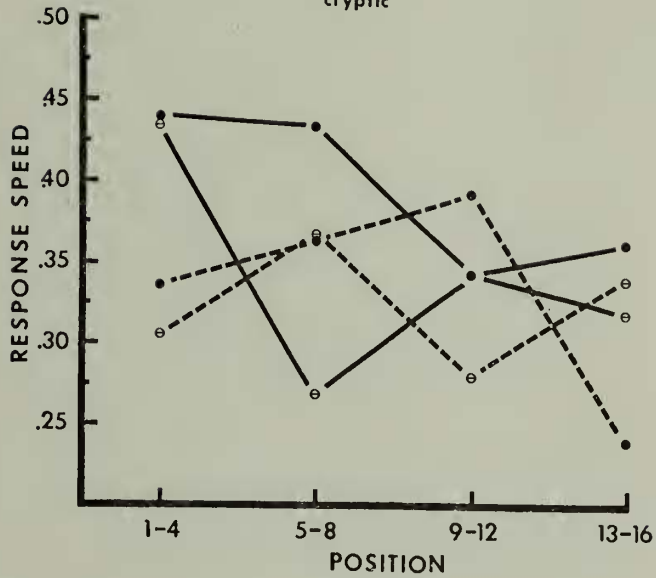
ANOVA of percentage correct on negative trials in the experimental blocks revealed no significant overall difference in performance between RUNS and NON-RUNS. The jays responded at a mean of 83.0% correct to negative

FACE PAGE FOR FIGURE 10

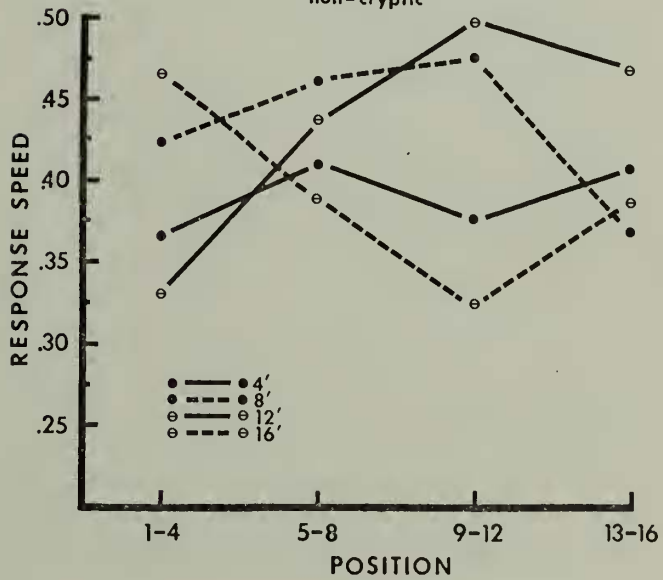
Figure 10. Mean response speed to positive slides as a function of crypticity, distance from which the slides were taken, and position of the slides in the experimental block. (Experiment 2)

C. relecta - C. relecta

cryptic



non-cryptic



slides in RUNS, and at a mean of 79.0% correct in NON-RUNS. In addition, there was no significant effect of run type as a function of the type of background in the negative slide. The jays responded at a mean of 74.5% correct to negative slides of oak in the RUN condition, at 74.2% correct to the same slides in the NON-RUN condition; at 91.7% correct to negative slides of non-bark in the RUN condition, and at 84.8% correct to these same slides in the NON-RUN condition.

There was a small non-significant difference in performance between the RUN and NON-RUN conditions. Percentage correct on negative slides decreased as a function of position, $F(3,12) = 6.08$, $p < .01$, from a high of 89.0% correct in Positions 1-4 to a low of 70.9% correct in positions 13-16. Furthermore, the effect of position upon percentage correct varied with run type and distance.

Figure 11 presents the mean percentage correct on negative slides as a function of run type, position, and distance. In the RUN condition, there was a large decrease in percentage correct across position on slides taken at 12 and 16 feet, while there were smaller decreases across position on slides taken at 4 and 8 feet. In the NON-RUN condition, there was a large decrease in percentage correct across positions 5 - 16 on slides taken at 12 feet, while there were no consistent increases or decreases in performance, across position, on slides taken at 4, 8, and 16 feet. These differential effects upon performance as a function of these factors resulted in a significant interaction of Run type X Distance, $F(3,12) = 6.25$, $p < .01$; Distance X Position, $F(9,36) = 3.24$, $p < .01$; and Run type X Distance X Position, $F(9,36) = 3.63$, $p < .005$.

ANOVA of performance in terms of response speed to negative slides revealed no effects of run type, back-

ground in the slide, or position of the slide in the experimental block. The jays responded to negative slides in the RUN condition at a mean response speed of .205, and at .210 in the NON-RUN condition. Mean response speed to negative slides containing the oak background was .199, while the mean response speed to slides containing the non-bark background was .218. This difference in response speed was not statistically significant.

There was a small decrease in response speed across position of the slides. The jays responded at a mean speed of .217 to slides in positions 1-4, at .215 in positions 5-8, at .213 in positions 9-12, and at .184 in positions 13-16. However, this decrease in response speed across position was not significant.

Discussion

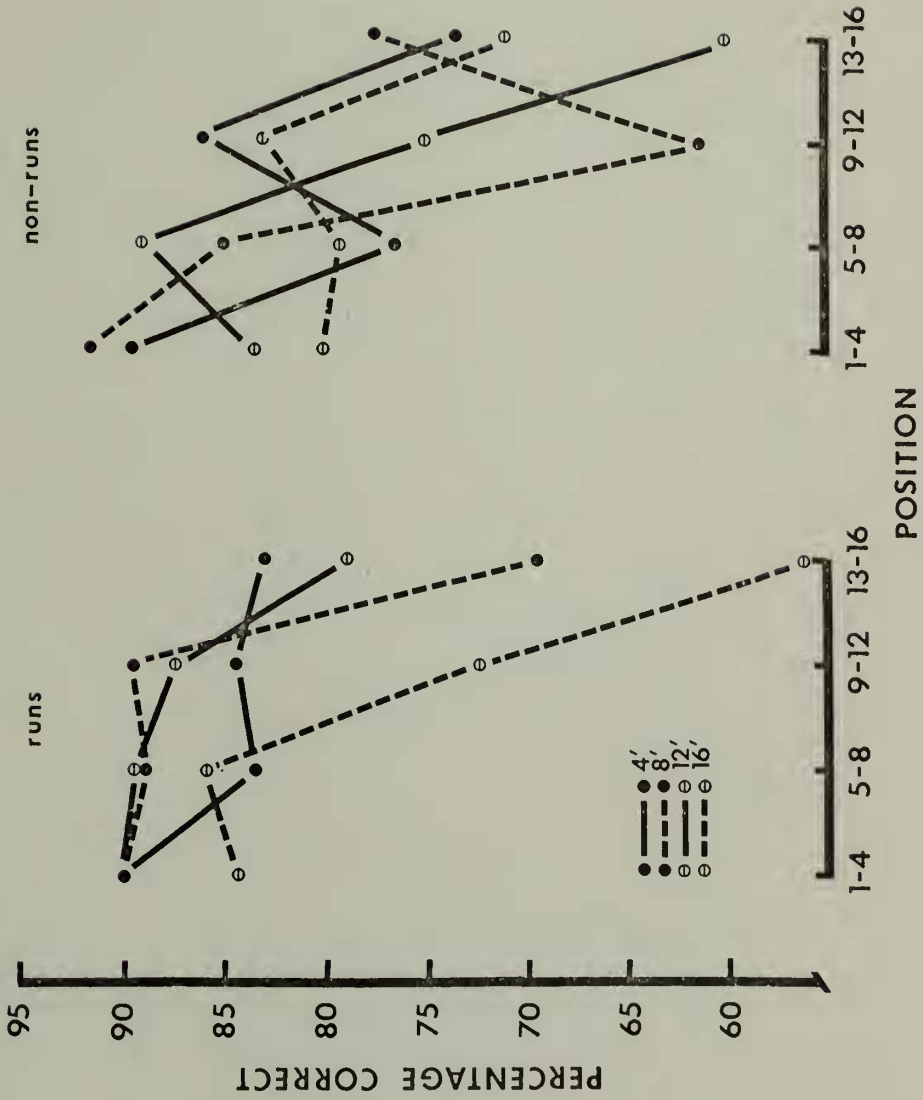
The most important finding of this experiment was the dramatic effect of run type, upon accuracy of detection of the moths which occurred only in the cryptic condition. The fact that the jays detected cryptic moths better when presented with runs of one species than with non-runs of two species is consistent with the results of Croze's (1970) experiment. The results of these two studies clearly suggest the operation of some mechanism which produces increased detection of cryptic prey when a predator searches for one prey type. However, the components of the visual stimulus configuration of the prey which gives rise to these changes in detection accuracy are not directly evident from the results of this experiment.

The results produced by the NON-RUN condition in this study indirectly provide suggestions as to the visual components of the prey which may be responsible for these changes in detection. In this study, the NON-RUN condition not only consisted of species which differ visually,

FACE PAGE FOR FIGURE 11

Figure 11. Mean percentage correct on negative slides as a function of run type, distance from which the slides were taken, and position of the slides in the experimental blocks. (Experiment 2)

C. relecta - *C. relecta*



but also consisted of changes in background (birch and oak) from trial to trial. Therefore, it cannot be determined, on the basis of these data, which factor was most important in producing the decreased accuracy of detection in NON-RUNS: the presentation of two visually different species, or the presentation of the two different backgrounds upon which these species were cryptic. Croze used three visually different prey types in his study, but all three types were cryptic on the same substrate. His result suggests that presentation of visually different prey types may produce reduced detection accuracy. However, the effect of a variable substrate cannot be eliminated as a component of this effect upon detection. On the basis of the results of the non-cryptic conditions, it may be argued that the variation in background during cryptic NON-RUNS was the critical factor producing reduced detection. Under non-cryptic conditions, both species always occurred on the same artificial background, and there was no significant difference in performance between RUN and NON-RUN conditions. However, since non-cryptic conditions result in very high levels of detection accuracy, in both RUNS and NON-RUNS, no conclusion about the effects of background cues can be made.

The question of which factor was critical in producing reduced accuracy of detection in cryptic NON-RUNS is important in determining exactly how different two morphs can be (morphologically and behaviorally) for there to be a consequent selective advantage against predation. Of course, the relative densities of the morphs are undoubtedly critical in maintaining such an advantage, and this factor presents questions that cannot be addressed in the present experiment. Poulton (1890) suggested that polymorphism confers an advantage against predation if there

is wide divergence in coloration. This hypothesis is supported by the results of this experiment and by that of Croze (1970). It seems feasible that cryptic morphs differing greatly in coloration will have a selective advantage against predation based on that difference. However, this study suggests that selection of different resting substrates by the morphs may also be an important factor in the defense against predation.

There is no direct evidence of search image effects in these data, although performance in CRYPTIC RUNS was better than in NON-CRYPTIC RUNS. The overall increase in percentage correct in CRYPTIC RUNS across position of the slides in the run was not large enough to conclude that a search image had been formed. In addition, the general decrease in percentage correct on negative slides and the decrease in response speed in positions 13-16 suggests, as did the results of the first experiment, that search image formation may have been inhibited by both the inconsistency of orientation of the moths in RUN conditions and the long length of the test sessions.

The next experiment investigated search image formation when the orientation of the moths was consistent, and during shorter sessions, to eliminate potential satiation effects.

Experiment 3

The third experiment investigated search image formation with shorter runs, in which the moths occurred only in their species-typical orientation. With consistent orientation of the moths in positive trials of the runs, a search image could be formed for the more specific stimulus configuration, and therefore, could develop more readily than when the orientation varies. In this experiment, C. resecta, an oak mimic, and C. relictata, a birch mimic, were used to maximize the difference between

prey species in the non-run conditions. In addition, because the results of Experiments 1 and 2 showed no effect of run type upon performance when the moths were conspicuous, this experiment investigated search image formation only when the moths occurred under cryptic conditions.

Method

A set of 32 experimental slides was used in this study: 8 slides containing C. relictata head up on birch, with 8 matched negative slides, and 8 slides containing C. relectata head down on oak, with 8 matched negative slides. Each species occurred twice on its matching background at each of 4 distances (4, 8, 12 and 16 feet).

The jays were exposed to these slides in sessions of 24 trials, 2 sessions a day (with 1.5 hours between sessions) for 12 days. Each session included 16 slides from the above set, and 8 slides (4 positive, 4 negative) randomly chosen from the set described by Pietrewicz (1975). Within each session, there was one experimental block composed of 8 positive and 8 corresponding matched negative slides from the set described above. The experimental blocks began equally often on Trials 3, 4, or 5 of the session, in order to make the start of the experimental block unpredictable. The exact trial on which the experimental block began was randomized with the exception that no two experimental blocks occurring on the same day of training began on the same trial number.

Each experimental block of trials represented one of the following conditions: RUNS - the 8 positive slides all contained the same species of cryptic moth; NON-RUNS - 4 positive slides contained C. relictata and 4 positive slides contained C. relectata. Thus, there were 3 major types of slide presentation in the experimental blocks:

RUN of C. relictata on birch; RUN of C. retecta on oak; and NON-RUN of C. relictata and C. retecta intermixed.

Each day of testing was designated a RUN day or a NON-RUN day. On RUN days, one session contained a run of C. retecta, and the other session contained a run of C. relictata in the experimental block of trials. The order of presentation of RUN types was randomized, so that a run of C. retecta and a run C. relictata occurred equally often in Session 1 and Session 2 of the 12 days of testing. On NON-RUN days, both sessions contained the NON-RUN experimental blocks. There was a total of 8 RUN days, in which there was a total of 8 sessions containing runs of C. retecta and 8 sessions containing runs of C. relictata. There were 4 NON-RUN days, in which there was a total of 8 sessions containing non-runs. The order of presentation of RUN and NON-RUN days was randomized.

The order of presentation of slides within each experimental block of trials was counterbalanced in the following manner. Order of presentation of positive and negative slides was random with the exception that each experimental block began with a positive slide, and no more than 3 consecutive positive or negative slides occurred. The positions of the 8 positive slides within the experimental block of trials were designated positions 1-8, and within each type of experimental block (e.g. RUNS of C. relictata) positive slides were counterbalanced so that each distance (4, 8, 12, and 16 feet) occurred equally often in each of the 8 positions. The positions of the 8 negative slides were counterbalanced so that each distance occurred equally as often in each of the 8 negative slide positions. In addition, for both positive and negative slides within any experimental block, each distance (4, 8, 12, and 16 feet) occurred once in positions 1-4, and once in positions

5-8, so that a consecutive string of positive or negative slides from any one distance was avoided.

Results

The jays maintained high levels of performance during Experiment 3, responding at a mean of 33.6% correct on positive trials, and at 82.9% correct on negative trials.

For Experiment 3, subsequent post-hoc comparisons (Dunnett's test) of performance are presented in Tables 17 and 18 of Appendix A. Individual data of the birds are presented in Appendix B.

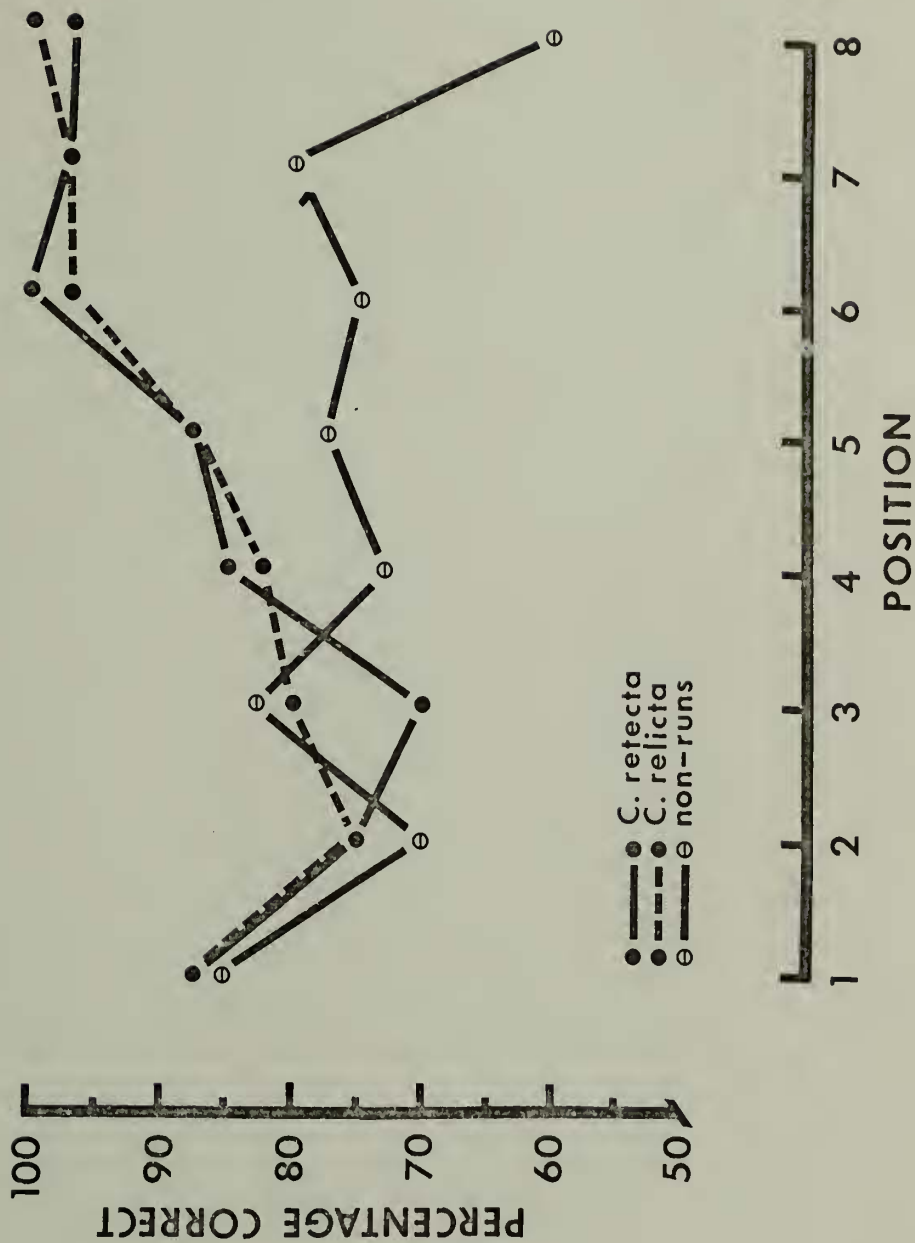
Performance on positive trials of experimental blocks

The condition under which the slides were presented had a large effect upon accuracy of detection of the moths. The jays responded at a mean of 87.8% correct on RUNS of C. retecta, at 38.1% correct on RUNS of C. relictata, and at 75.0% correct on NON-RUNS. The overall effect of condition upon percentage correct was significant, $F(2,8) = 7.68$, $p < .025$. In addition, response speed was somewhat faster in RUN conditions. The jays responded at a mean speed of .431 in RUNS of C. retecta, at .456 in RUNS of C. relictata, and at .415 in NON-RUNS. These differences, however, were not large enough to produce a significant main effect of Condition upon response speed, $F(2,8) = 1.48$, $p > .10$.

The position of the slide in the experimental block had a large effect upon percentage correct but only in the RUN condition. Figure 12 presents the mean percentage correct on positive trials as a function of the position of the slide and the condition within which the slides were presented. There was an increase in percentage correct across position in both RUN (C. relictata and C. retecta) conditions. There was no consistent increase in percentage

FACE PAGE FOR FIGURE 12

Figure 12. Mean percentage correct on positive slides as a function of the condition within which the slides were presented, and the position of the slide in the experimental blocks. (Experiment 3)



correct across position in NON-RUNS. The main effect of position upon percentage correct was significant, $F(3,12) = 11.42$, $p < .005$, and there was a significant interaction of Condition (RUN or NON-RUN) X Position, $F(6,24) = 4.44$, $p < .005$. Subsequent post-hoc comparisons (Dunnett's tests) revealed a significant difference in percentage correct between C. resecta RUNS and NON-RUNS at Positions 5-6, $D(24) = 2.16$, $p < .05$; and Positions 7-8, $D(24) = 3.59$, $p < .005$. In addition, there was a significant difference between C. relictata RUNS and NON-RUNS at Positions 7-8, $D(24) = 3.47$, $p < .005$.

The distance from which the slides were taken also had a large effect upon percentage correct. The jays responded at a mean of 93.8% correct on slides taken at 4 feet, at 83.3% correct at 8 feet, at 81.3% correct at 12 feet, and at 76.3% correct at 16 feet. This decrease in percentage correct with increased distance in the slides was significant, $F(3,12) = 11.91$, $p < .001$. There was also a decrease in response speed as distance in the slides increased, $F(3,12) = 4.32$, $p < .05$. The jays responded at a mean speed of .480 to slides taken at 4 feet, .460 at 8 feet, .431 at 12 feet, and at .366 at 16 feet.

Performance on negative trials of experimental blocks

The factors that affected percentage correct on positive slides similarly affected percentage correct on negative slides. The jays responded to negative slides within C. resectata RUNS at a mean of 87.5% correct, to slides within C. relictata RUNS at 85.0% correct, and to slides within NON-RUNS at 76.3% correct. The effect of condition of presentation upon percentage correct on negative slides was significant, $F(2,8) = 17.60$, $p < .005$. There was also a significant effect of condition upon response speed on negative trials, $F(2,8) = 4.80$, $p < .05$. The jays responded

at a mean speed of .281 to negative slides within C. retecta RUNS, at .263 within C. relictata RUNS, and at .288 within NON-RUNS.

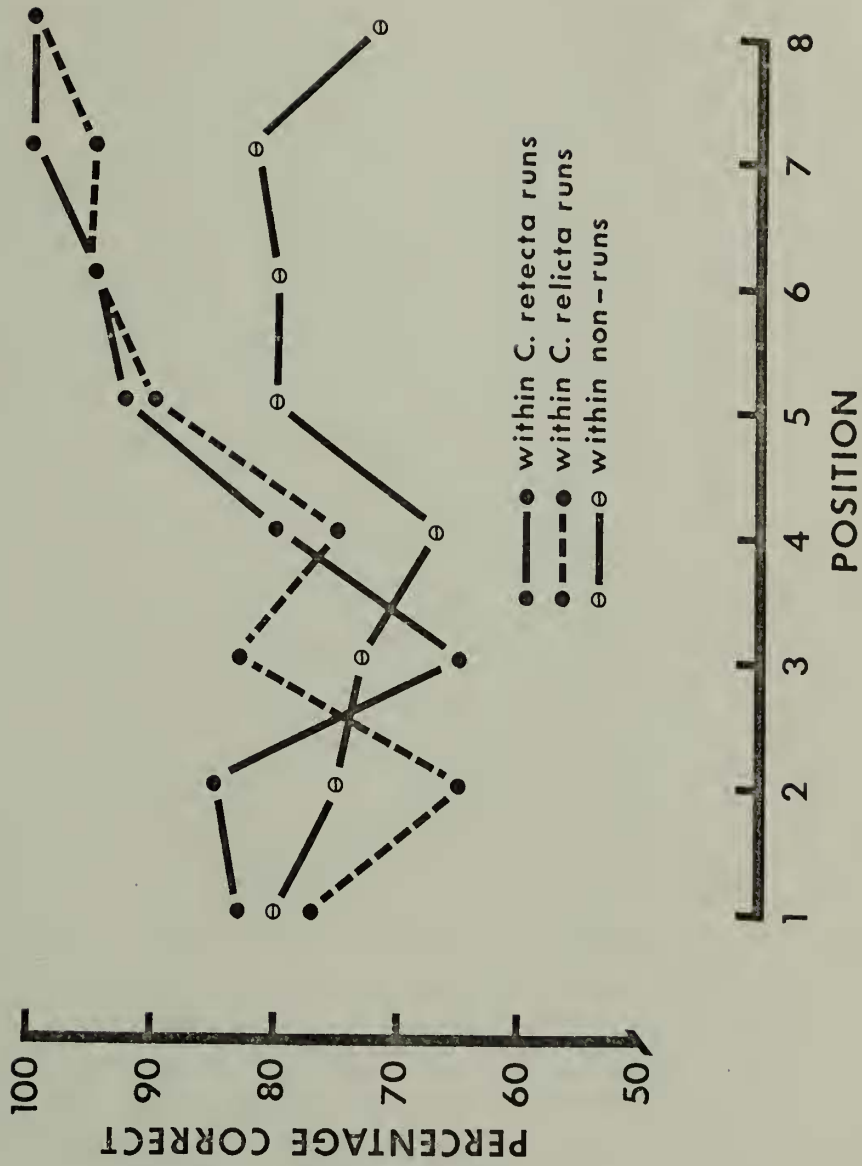
There was a general increase in percentage correct across position of the negative slides in experimental blocks, $F(3,12) = 13.15$, $p < .001$, which was most dramatic within the RUN conditions. Figure 13 presents percentage correct on negative slides as a function of position of the slide within each experimental condition. In the RUN conditions, the jays responded close to 100% correct on negative slides in positions 7 and 8, while performance on negative slides within the NON-RUN condition did not exceed 82.5% correct in any position. This differential effect of position upon percentage correct as a function of condition (RUNS and NON-RUNS) resulted in a significant Condition X Position interaction, $F(6,24) = 3.04$, $p < .025$. Subsequent post-hoc comparisons (Dunnett's tests) revealed a significant difference in percentage correct between C. retecta RUNS and NON-RUNS at Positions 7-8, $D(24) = 2.11$, $p < .05$. In addition, there was a significant difference in percentage correct between C. relictata RUNS and NON-RUNS at Positions 7-8, $D(24) = 1.97$, $p < .05$.

There was a decrease in percentage correct on negative slides with increased distance from which the slides were taken, $F(3,12) = 10.96$, $p < .001$. The jays responded at 89.6% correct to negative slides taken at 4 feet, 85.4% correct at 8 feet, 80.0% correct at 12 feet, and 76.7% correct at 16 feet.

It should be noted that the effects shown here of position of the slides and the condition (RUN or NON-RUN) in which they were presented upon percentage correct, for both positive and negative trials, were not only reflected in the grouped data. These effects were also reflected in

FACE PAGE FOR FIGURE 13

Figure 13. Mean percentage correct on negative slides as a function of the condition within which the slides were presented and the position of the slides in the experimental blocks. (Experiment 3)



the performance of the individual birds (See Appendix B).

Discussion

These data strongly suggest that the jays adopted a specific search image when presented with runs of one moth species. The dramatic improvement in accuracy of detection with consecutive encounters with one prey type, accompanied by the absence of this effect with the same slides in NON-RUN conditions, supports this conclusion. In addition, these data suggest that consistent orientation of the stimulus configuration represented by the moths is necessary for the formation of a specific search image.

It is interesting to note, however, the similar increase in percentage correct across position of the negative slides. This result indicates that the possible components of the search image should be carefully considered. It may be argued that the increase in accuracy of detecting both the presence and absence of moths might have been due to an increased short-term familiarity with one substrate, rather than a focus on the stimulus configurations represented by the moths. Croze (1970) argued that search image involves attending to the prey type as well as the prey's background, and that the releasing stimulus situation probably includes properties of the background. These data support the hypothesis that background cues upon which cryptic prey rest is an important component of the jays' search. If the jays were not attending to visual characteristics of the background, but rather, were only attending to the specific stimulus configuration represented by the cryptic moth, then no increase in performance on negative slides should have occurred; the jays should have detected the absence of the moths as readily in position 1 as in position 8. Therefore, with consecutive encounters with similar, vacant substrates, the jays may

have located and scanned the substrate more efficiently with each encounter. Perhaps then, with consecutive encounters with one moth species, the search image itself increased in strength, and the jays thus more accurately detected the absence of this image on the substrate.

In this study, the composition of the RUNS conditions may have facilitated the increased detection of the absence of the moths. Because C. resecta occurred only on oak, and C. relictata occurred only on birch, the substrate type presented in the slide consistently predicted the moth species for which the jays had to search. Therefore, the development of the search image and the concurrent availability of a substrate which predicted the possible presence of the species for which the search image was formed, may interact to increase the efficiency of the search. In the wild, these species of moth rarely rest on non-matching substrates. Thus, it seems reasonable to assume that learning the typical location of individual prey types concurrently with formation of the search image would be an efficient search strategy not only in this laboratory situation, but also in the field. The fact that there was no increase in performance on negative slides in the NON-RUN condition, where substrate also predicted moth type, suggests that learning the location of individual prey types alone does not give rise to increased accuracy of detection. The importance of the cues provided by the substrate in search image formation were further investigated in the next experiment.

Although these data on performance on negative slides suggest that search image results in an increased detection of the absence of the moth the increased accuracy of detecting the absence of a moth in the slides may have been directly the result of these testing procedures, and should

not be assumed to necessarily occur in the wild. These procedures required the jays to emit a discrete response to the absence of a moth, and this response differs qualitatively from the response required to the presence of a moth. In the wild predators may not overtly respond to the absence of a prey item for which they are searching. Thus, any conclusions made on the basis of responses to negative slides should be tentative.

An additional point on the nature of the experimental methods used here should be considered. Although effects interpretable as search image were produced by RUN conditions and not by NON-RUN conditions, it cannot be concluded that any NON-RUN condition, where two species of prey are intermixed, would not also result in search image effects. In this experiment, RUNS consisted of 8 "encounters" with a particular prey item, but in NON-RUNS, this same prey item occurred only 4 times. It is possible that a search image could be formed for one prey type in NON-RUNS, if NON-RUNS contained the same number of presentations of one prey type as did the RUNS condition. However, in view of Croze's (1970) study and that of other studies on search image, this possibility does not seem likely. The advantage of using a search image, it seems, would be to increase the ability to detect cryptic prey within a relatively small number of encounters. This research, therefore, focused upon the formation of search image within a fixed number of encounters with any prey type. The possibility of search image formation for one prey type under conditions where there are numerous encounters with more than one prey type is not within the scope of the present research, but would be an interesting question for future research.

In Experiment 3, two visually different species,

which were cryptic on different backgrounds, were used. Therefore, no conclusions could be made about which factor, different coloration or different resting substrate, was most important in producing reduced detection accuracy in NON-RUNS. The ideal experiment to investigate this question would involve the use of two differently colored species which are cryptic on the same background. However, since slides of such species were not available, the next experiment tested search image formation with two species similar in coloration and cryptic on the same background, using procedures similar to those that successfully produced search image effects in the present experiment.

Experiment 4

Experiment 4 tested search image formation in the same manner as Experiment 3, but using two species, C. re-
tecta and C. cara, which are cryptic on the same back-
ground.

In this experiment, C. retecta was presented consistently head-down on oak, and C. cara was consistently presented head-up on oak. Thus, the NON-RUN condition here differed from the NON-RUN condition in Experiment 3 in the following ways: the same substrate appeared in all slides, thus eliminating substrate as a predictor of prey type; the two moth species were visually similar in coloration, although orientation of the moth still varied.

If the NON-RUN condition in this experiment, compared with the RUN condition, reduced accuracy of detection, this would suggest that differences in coloration and resting substrate of prey items inhibit formation of the search image, and that differences in body orientation are not critical for search image formation. Therefore, such a result would suggest that some similarity in coloration and resting substrate between two species would facilitate

detection accuracy, and presumably, search image formation. If, on the other hand, the NON-RUN condition here resulted in reduced detection accuracy compared to the RUN condition, this result would suggest that differences in orientation and slight differences in coloration between two species, despite similar substrate choice, are sufficient to inhibit search image formation, and thus searching consistently on one substrate alone is not sufficient to produce search image effects.

Method

Experiment 4 was conducted in exactly the same manner as Experiment 3, except that a corresponding set of slides of C. cara, head-up on oak, was substituted for the set of slides of C. relictata. The same set of slides of C. relectata, head-down on oak, from Experiment 3 was used in this experiment.

Results

The jays retained overall high levels of performance in Experiment 4, responding at a mean of 83.5% correct on positive slides, and at 82.0% correct on negative slides.

Performance on positive slides of experimental blocks

The type of condition, C. relectata RUNS, C. cara RUNS, and NON-RUNS, had no significant effect upon percentage correct on positive slides. The jays responded at a mean of 85.0% correct on C. relectata RUNS, at 85.3% correct on C. cara RUNS, and at 80.3% correct on NON-RUNS. The most important factor affecting percentage correct in the experimental blocks was the position of the slide. There was an overall increase in percentage correct across position of the slides, $F(3,12) = 11.88, p < .001$.

Figure 14 presents percentage correct on positive slides as a function of position of the slides within the

three experimental conditions. Although percentage correct in the RUN conditions was higher on slides in positions 6, 7, and 8 than in the NON-RUNS, there was no significant interaction between condition and position, $F(6,24) = 1.83$, $p > .10$.

Response speed to positive slides increased as a function of position of the slides in the experimental block. The jays responded at a mean speed of .417 to slides in positions 1-2, at .425 in positions 3-4, at .456 in positions 5-6, and at .453 in positions 7-8. However, the effect of position upon response speed was not significant, $F(3,12) = 2.27$, $p > .10$.

Performance on negative trials of experimental blocks.

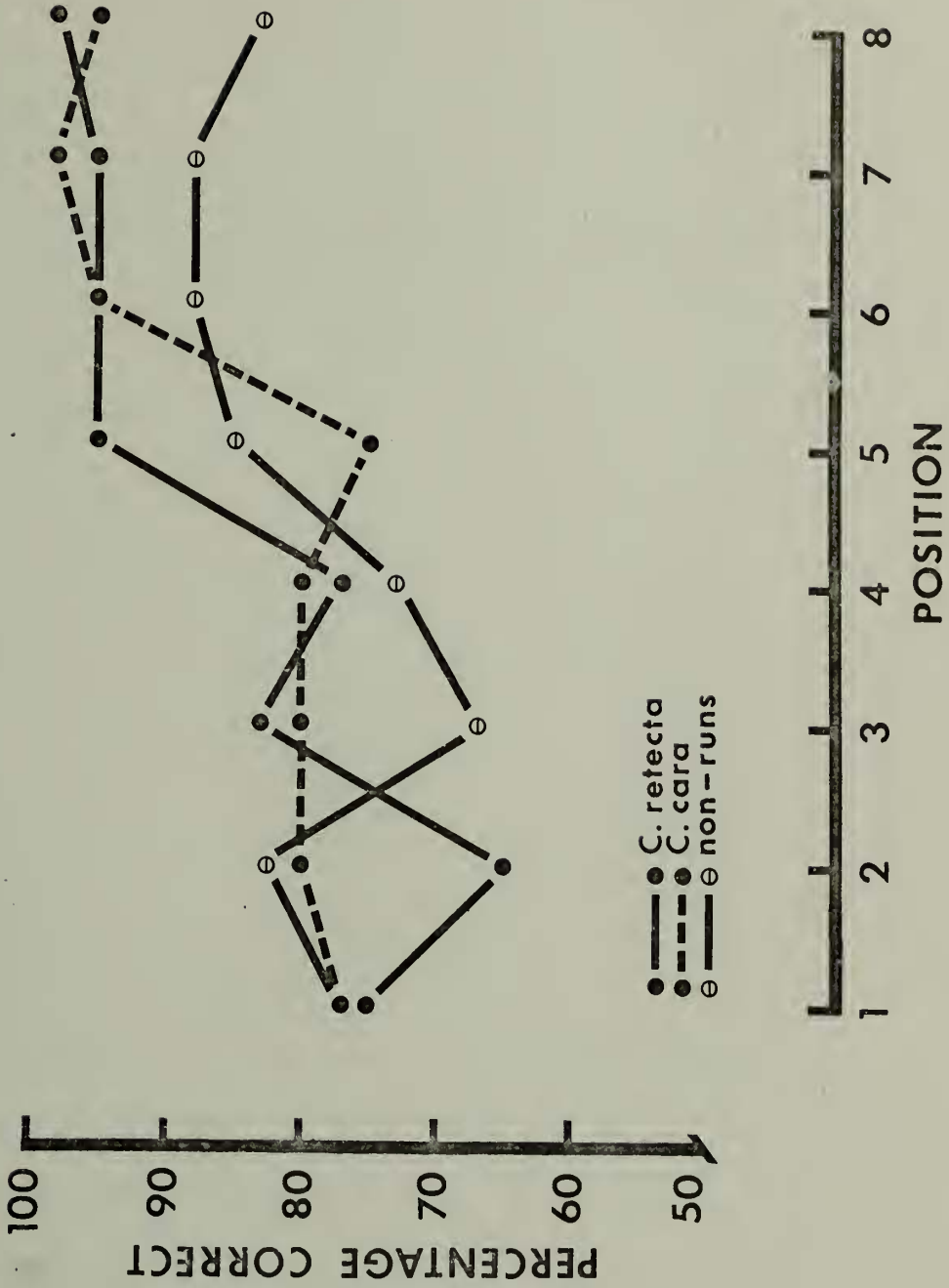
There was no significant effect of condition (RUN or NON-RUN) upon percentage correct on negative slides, although percentage correct was slightly lower in NON-RUNS than in the RUN conditions. The jays responded at a mean of 86.3% correct to negative slides within C. cara RUNS, at 81.9% correct in C. retecta RUNS, and at 77.8% correct in NON-RUNS.

Figure 15 presents percentage correct on negative slides as a function of position within the three experimental conditions. There was an overall increase in percentage correct across position in the experimental block, $F(3,12) = 18.77$, $p < .001$. This increase in percentage correct across position was similar in both RUNS and NON-RUNS, as there was no significant Condition X Position interaction, $F(6,24) = .72$, $p > .10$. Neither position of the slide or condition had an effect upon response speed to negative slides.

As in Experiment 3, the effects of position of slides was reflected not only in the grouped data, but also in the performance of the individual birds, on both

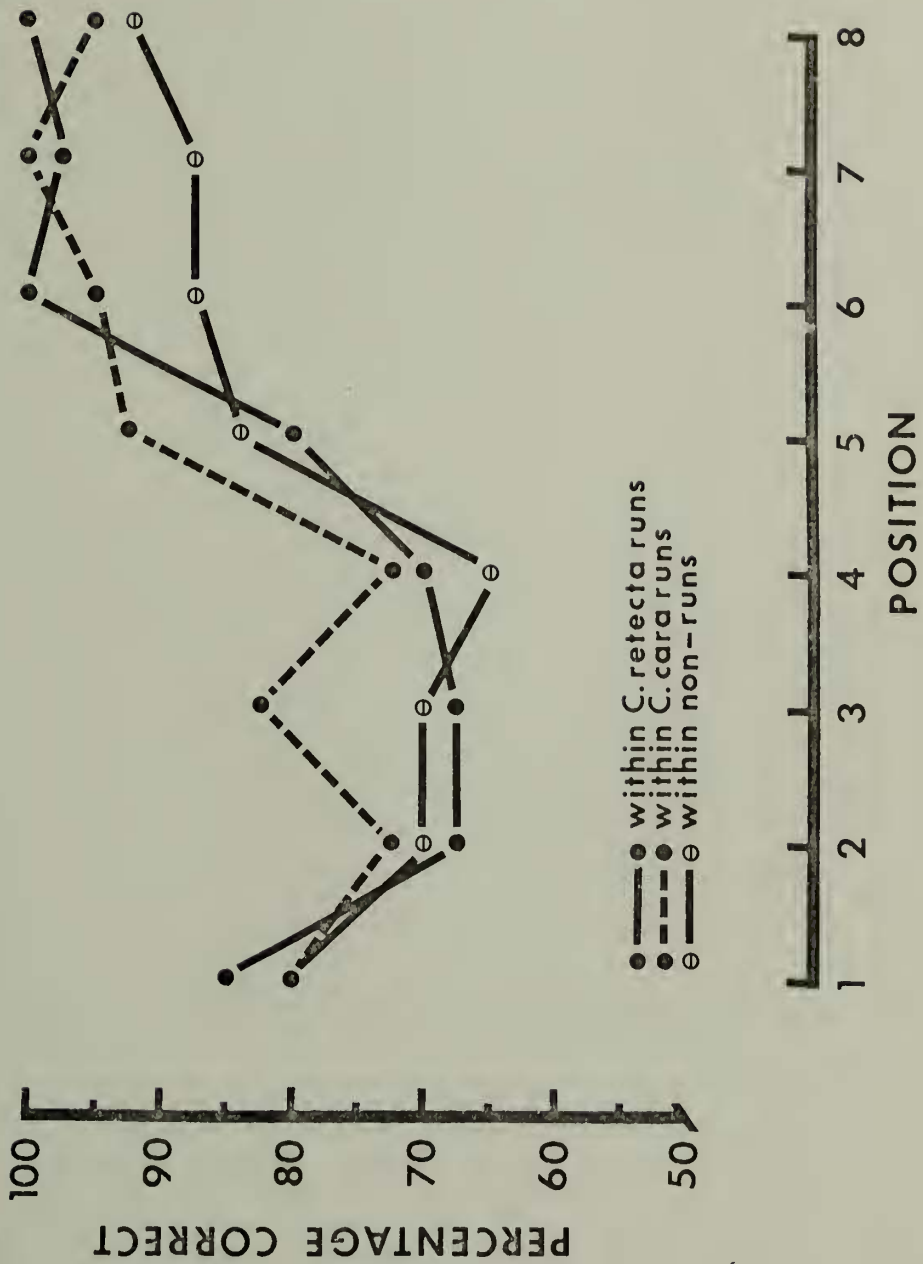
FACE PAGE FOR FIGURE 14

Figure 14. Mean percentage correct on positive slides as a function of condition of presentation and position of the slides in the experimental blocks. (Experiment 4)



FACE PAGE FOR FIGURE 15

Figure 15. Mean percentage correct on negative slides as a function of condition of presentation and position of the slides in the experimental blocks. (Experiment 4)



positive and negative slides (see Appendix B).

Discussion

These data indicate that the jays formed a specific search image under both the RUN and NON-RUN condition. Since the overall position effect was significant, this result indicates that the jays formed a search image under both these conditions. These data, and the data from Experiment 1, suggest that C. cara on oak and C. retecta on oak may have stimulus components in common to which the birds respond, and for which a search image may develop, in spite of their presentation in different orientations. These data indicate, then, that detection is facilitated when one cryptic prey type is consistently presented in one orientation. However, if two prey species, similar in appearance and cryptic on the same background, are presented, a weak search image may be formed for the stimulus configuration common to these two species, or a search image formed for one species may generalize to a similar colored species, even on a different orientation.

On the basis of the data from this experiment, the absence of search image effects in RUN conditions of Experiments 1 and 2 cannot be attributed to the variation in orientation of the moths within runs of one prey type. Rather, the absence of such effects suggests that other aspects of the procedure, such as the long sessions, were responsible for these results. In addition, these results suggest that consistency of orientation is not absolutely necessary for the formation of search image. Although it appears likely that consistency of orientation will facilitate search image formation, it apparently is not a necessary condition.

It may be argued that the results of the NON-RUN condition in this experiment are inconsistent with the

results of the NON-RUN condition in Experiment 1. In both experiments, NON-RUNS contained C. cara and C. resecta on oak; under this condition, Experiment 3 showed evidence of search image formation, while Experiment 1 did not. However, it should be noted that the positive slides in NON-RUNS of Experiment 1 actually represented 4 stimulus configurations: C. cara head-up, C. cara head-down, C. resecta head-up, and C. resecta head-down. Positive slides of NON-RUNS in Experiment 4 actually represented 2 stimulus configurations: C. resecta head-down, and C. cara head-up. Detection of cryptic prey may be best facilitated when: coloration is consistent, there is little variation in body orientation, and choice of resting substrate is consistent. Search image formation, as evidenced by an increase in detection accuracy, may also occur, but may be weaker when there is some variation in coloration and orientation is variable. Such effects do not occur when there is wide divergence in coloration between prey types and substrate choice varies between species.

The results of this experiment also show an increased ability of the jays to detect the absence of the moths across position in the experimental blocks. Again, it cannot be determined, on the basis of these data, whether the increases in accuracy of detection of the absence of the moths occur with a mechanism similar to that operating in positive slides. As stated earlier, the increased accuracy of detecting the absence of a moth may be due to a retention of the search image while negative slides are presented, or, it may be due to a separate mechanism forced into use by the response requirements in these procedures. If the former hypothesis is the case, then these data would suggest that the stimulus cues provided by the

substrate are a critical component of the search image and allow retention of the search image during negative slides.

General Discussion

The results of this research provide the first direct demonstration of search image formation as defined by Dawkins (1971a): an increased ability to detect cryptic, familiar prey following a few consecutive encounters with that prey item. This evidence for search image in the blue jay is not confounded with prey preferences, differences in palatability of the prey, ease of capture or handling time, or avoidance of an unfamiliar prey item. Such factors, in the past, have interfered with the interpretation of data purporting to provide evidence for search image formation (Krebs, 1973). This research also provides evidence that visual cues provided by the substrate upon which cryptic prey rest are important in search image formation, a factor which has been relatively ignored in previous research. Furthermore, these results demonstrate that blue jays develop an increased ability to detect the absence of a moth, concurrently with search image formation for that moth, although this result may be specific to the procedures utilized here. However, the development of an increased ability to detect the absence of a prey item during search image formation suggests an additional way in which runs of single prey types may increase predator efficiency. The more quickly a predator can recognize the absence of prey, the more quickly he can begin to examine potentially more profitable areas.

This research has also demonstrated that operant procedures can be used to simulate the presentation of monomorphic and polymorphic prey populations, by controlling

the prey types presented in a sequence of slides presented to the birds. The data generated with this procedure, in addition, support the hypothesis that visual polymorphisms confer an advantage upon cryptic prey, making each morph less likely to be detected by a predator. However, these data have also raised a number of questions on exactly how different two morphs must be in order to interfere with their detection by jays. These data do suggest that wide divergence in coloration and substrate choice are important factors in maintaining a defense against predation.

Characteristics of search image formation

With these procedures, search image formation occurred when the jays were presented with runs of slides containing a single moth species, intermixed with matching negative slides. The increased accuracy of detection with consecutive encounters with one prey type, however, was not evident until at least the fifth presentation of a particular species of moth, indicating that five or more encounters were necessary before a search image was formed. It may be argued that interjection of negative slides between positive slides resulted in the rather gradual formation of the search image. However, this explanation seems unlikely to have been the cause of the seemingly slow search image formation. In the present research, each positive slide in a RUN of one prey type was counted as an "encounter", whether or not the moth in the slide was detected, and indeed, some of the moths in the first few encounters went undetected. Since an undetected moth cannot technically be considered a true "encounter", it is reasonable to assume that changes in the ability to detect the moths in RUNS occurred more quickly than reflected by the data. If the undetected moths in positive slides were counted as negatives, the data would show more rapid formation of

of the search image.

There are several aspects of the present data which suggest that with formation of the search image, the search image itself increases in strength, or becomes more refined, to allow better accuracy of detection of the moths, a process which may occur through increased attention to the stimulus configuration represented by the moth. First, the absence of a sharp increase in percentage correct from one position to the next in RUNS of one prey type suggests that search image does not suddenly appear in any one particular encounter. Rather, the search image seems to gradually develop, or become refined, from encounter to encounter. Second, the gradual increase in percentage correct across negative trials within RUN conditions lends support to this hypothesis. It seems plausible that such effects would be due to an increased attention to some portion of the stimulus configuration associated with the presence of the moth.

The suggestion that with development of a search image, the jays responded with increased attention to the stimulus configuration of the moth can account for the effects of RUNS upon response speed in Experiments 3 and 4. In these experiments, the mean response speed on positive slides corresponds to a response latency of 2.3 seconds. The mean response speed on negative slides corresponds to a response latency of 3.8 seconds. This difference in response speed on positive and negative slides indicates that the jays may have been limiting the time spent searching for moths in the slides. On positive slides, the jays may have terminated their search when a moth was not detected within a specific time interval. This same difference in response speed between positive and negative slides was found by Pietrewicz (1975), and occurred in

the present experiments in both RUN and NON-RUN conditions. However, some interesting effects of RUNS and NON-RUNS upon response speed on negative slides occurred in Experiment 3. Experiment 3 was the only experiment which produced a difference in detection accuracy on RUNS and NON-RUNS which could be attributed to search image formation. RUNS resulted in search image formation, while NON-RUNS did not. On negative slides in this experiment, response speed was significantly slower in NON-RUNS than in RUNS. Thus, search image formation in RUNS resulted in faster, in addition to more accurate, detection of the absence of the moths. It seems likely, then, that the search image was retained during the presentation of negative slides, and operated to increase the speed with which the jays detected its absence. Without search image formation, then, the jays apparently must scan the substrate for a longer period of time before deciding to terminate the search.

In summary, search image formation seems to be a somewhat gradual increase in attention to some aspect of the stimulus configuration which represents the resting moths, or in other words, an increase in the strength or specificity of the search image. When a search image is formed, it is subsequently retained in the moth's absence, and results in faster and more accurate detection of the absence of this image.

It should be noted, however, that in these experiments the search image was retained during presentation of negative slides containing the same substrates that were present in positive slides. Search images might not be retained during negative trials which displayed a substrate markedly different from that which the prey normally rests upon. It would be important, in the future, to test whether presentation of negative slides containing an in-

appropriate background would disrupt search image formation. If such a result occurred, it would indicate that a restriction of the area searched might be a necessary condition for search image formation. This result would also suggest a connection between patch selection (krebs, 1973) and search image under field conditions.

Specificity of the search image

The present research found that search image is formed with consecutive encounters with one cryptic prey species, and this result suggests that a search image is formed for a very specific stimulus configuration. On the other hand, search image formation was also observed when two species, similar in coloration but occurring in different orientations, were successively presented on the same background. Although search image effects occurred under this condition, this search image did not produce levels of detection accuracy as high as those when the search image was formed for one species. These results suggest that a search image may vary in specificity. The more specific the stimulus configuration for which the search image is formed, the better the accuracy of detection. When the search image is formed for a less specific, or more variable, stimulus configuration, accuracy of detection is reduced. This conclusion is also supported by the results of performance on negative slides. Detection of the absence of the moths was more accurate when a search image was formed for one species than when a search image was formed with the presentation of two similar species. However, detection of the absence of the moths under these conditions was better than when no search image was formed.

The conclusion that the specificity of a search image can vary, and subsequently results in a variation in

detection accuracy, has important implications for the effects of polymorphism upon a predator's ability to detect cryptic prey. Since, in this study, differences in appearance between two cryptic prey consequently weakened search image formation, and resulted in lower levels of detectability of the prey, it can be concluded that the more divergent the visual polymorphism, the greater the defense against predation.

Effects of polymorphism upon the detection of cryptic prey

The present research has produced results consistent with those of Croze's (1970) experiments on the effects of visual polymorphism upon predation. The operant conditioning procedures provide a useful simulation of monomorphic and polymorphic populations in the field, by the variation of prey types presented in sets of slides. However, these data do not provide information on the effects of naturally occurring polymorphic forms upon the ability of blue jays to detect them. The simulated polymorphic populations in these experiments were constructed with slides of different species. Reduced detection of the moths resulted from presentation of two visually different species, cryptic on different backgrounds. It cannot be determined from the present data whether similar effects would occur, with these procedures, with natural polymorphic forms of prey. In addition, the frequency of the different "morphs" was equal in the sets of slides presented to the jays. Morphs of polymorphic Catocala species naturally occur with various frequencies in the field (Sargent, 1976) and, undoubtedly, the frequency with which a particular morph occurs in the wild, relative to the most common form, plays an important role in the advantage against predation which polymorphism confers upon a particular form (Clarke, 1962). The present research, however,

provides an excellent technique for the study of the effects of visual polymorphism upon detection of the morphs by blue jays. With these procedures, slides of various polymorphic forms can be presented and the frequency of occurrence of each morph can be carefully controlled to investigate the interacting effects of visual divergence upon detection by jays.

References

- Alcock, J. Cues used in searching for food by red-winged blackbirds. Behavior, 1973, 46, 174-188.
- Allen, J.A. and Clark, B. Evidence for apostatic selection by wild passerines. Nature, 1968, 220, 501-502.
- Beukema, J.J. Predation by the three-spined stickleback: The influence of hunger and experience. Behavior, 1968, 31, 1-126.
- Clarke, B. Balanced polymorphism and the diversity of sympatric species. In: Taxonomy and Geography (D. Nichols, Ed.). Systematics Association Publication, 1962, 44, (4).
- Croze, H. Search image in Carrion Crows. Zeitschrift fur Tierpsychologie, 1970, 5, 1-86.
- Dawkins, M. Perceptual changes in chicks: Another look at the "search image" concept. Animal Behaviour, 1971, 19, 566-574.
- Dawkins, M. Shifts of "attention" in chicks during feeding. Animal Behaviour, 1971, 19, 575-582.
- Gibb, J.A. L. Tinbergen's hypothesis of the role of specific search images. Ibis, 1962, 104, 106-111.
- Herrnstein, R.J. and Loveland, D.H. Complex visual concept in the pigeon. Science, 1964, 146, 549-551.
- Holling, C.S. The components of predation, as revealed by a study of small mammal predation of the European pine sawfly. Canadian Entomologist, 1959, 91, 293-332.
- Krebs, J.R. Behavioral aspects of predation. In: Perspectives in Ethology (P.P.G. Bateson and P.H. Klopfer, Eds.). Plenum Press: New York, 1973.

- Murton, R.K. The significance of a specific search image in the feeding behavior of the Wood pigeon. Behavior, 1971, 40, 10-42.
- Pietrewicz, A.T. Acquisition of differential responding to the presence or absence of moths in photographs by the Northern blue jay (Cyanocitta cristata). Master's Thesis, University of Massachusetts, 1975.
- Pietrewicz A.T. and Kamil, A.C. Visual detection of cryptic prey by blue jays (Cyanocitta cristata). Science, 1977, 195, 580-582.
- Poulton, E.B. The colours of animals. The International Scientific Series, Vol. 67. D. Appleton and Co.: New York, 1890.
- Royama, T. Factors governing the hunting behavior and selection of food by the Great Tit. Journal of Animal Ecology 1970, 39, 619-668.
- deRuiter, L. Some experiments on the camouflage of stick caterpillars. Behavior, 1952, 4, 222-232.
- Sargent, T.D. Background selections of geometrid and cotoxid moths. Science, 1966, 154, 1674-1675.
- Sargent, T.D. Cryptic moths: Effects on background selections of painting the circumocular scales. Science, 1968, 159, 100-101.
- Sargent, T.D. Behavioral adaptations of cryptic moths. III. Resting attitudes of two bark-like species, Melanophia canadria and Catocala ultronia. Animal Behavior, 1969, 17, 670-672.
- Sargent, T.D. Behavioral adaptations of cryptic moths. VI. Further experimental studies on bark-like species. Journal of the Lepidopterists Society, 1973, 27, 8-12.
- Sargent, T.D. Legion of Night: The Underwing Moths. Amherst: University of Massachusetts press, 1976.

Appendix A:

Tables 1-16: ANOVA of performance of percentage correct and response speed (Experiments 1-4)

Tables 17-18: Dunnett's tests of percentage correct on positive slides (Experiments 3-4)

Table 1

ANOVA of percentage correct on positive trials (EXPERIMENT 1)

<u>SV</u>	<u>df</u>	<u>SS</u>	<u>MS</u>	<u>F</u>	<u>SIG</u>
SUBJECTS (S)	4	7800.78	1950.20		
Runs (R)	1	125.00	125.00	.40	NS
S X R	4	1261.72	315.43		
Crypticity (C)	1	4882.81	4882.81	6.99	NS
S X C	4	2792.97	698.24		
Distance (D)	3	1945.31	648.44	2.99	NS
S X D	12	2605.47	217.12		
Position (P)	3	1539.06	513.02	3.08	NS
S X P	12	1996.09	166.34		
R X C	1	125.00	125.00	1.38	NS
R X D	3	1046.88	348.96	5.44	p<.025
C X D	3	539.06	179.69	.60	NS
R X P	3	1140.63	380.21	1.13	NS
C X P	3	2289.06	763.02	2.23	NS
D X P	9	2570.31	285.59	.87	NS
R X C X D	3	890.63	296.88	6.20	p<.01
R X C X P	3	1390.63	463.54	5.10	p<.025
R X D X P	9	2562.50	284.72	1.37	NS
C X D X P	9	4039.06	448.78	1.73	NS
S X R X C	4	363.28	90.82		
S X R X D	12	769.53	64.12		
S X C X D	12	3582.03	298.50		
S X R X P	12	4035.16	336.26		
S X D X P	36	11785.16	327.37		
S X C X P	12	4097.66	341.47		
S X R X C X D	12	574.22	47.85		
S X R X C X P	12	1089.84	90.82		
S X R X D X P	36	7496.10	208.22		
S X C X D X P	36	9339.84	259.44		
R X C X D X P	9	1843.75	204.86	1.03	NS
S X R X C X D X P	36	7160.16	198.89		
Total	319	93679.70			

Table 2

ANOVA of response speed on positive trials (EXPERIMENT 1)

<u>SV</u>	<u>df</u>	<u>SS</u>	<u>MS</u>	<u>F</u>	<u>SIG</u>
SUBJECTS (S)	4	7.815	1.953		
Runs (R)	1	.001	.001	.10	NS
S X R	4	.036	.009		
Crypticity (C)	1	.008	.088	1.08	NS
S X C	4	.328	.082		
Distance (D)	3	.104	.035	.87	NS
S X D	12	.480	.040		
Position (P)	3	.517	.172	6.46	p < .01
S X P	12	.320	.027		
R X C	1	.000	.000	.01	NS
R X D	3	.026	.009	.52	NS
C X D	3	.283	.094	3.07	NS
R X P	3	.052	.017	1.78	NS
C X P	3	.201	.067	5.37	p < .025
D X P	9	.210	.023	1.56	NS
R X C X D	3	.073	.024	3.09	NS
R X C X P	3	.092	.031	3.68	p < .05
R X D X P	9	.091	.010	.81	NS
C X D X P	9	.196	.022	1.27	NS
S X R X C	4	.034	.009		
S X R X D	12	.200	.017		
S X C X D	12	.370	.031		
S X R X P	12	.118	.010		
S X D X P	36	.537	.015		
S X C X P	12	.149	.013		
S X R X C X D	12	.095	.008		
S X R X C X P	12	.101	.008		
S X R X D X P	36	.450	.013		
S X C X D X P	36	.620	.017		
R X C X D X P	9	.404	.045	4.98	p < .001
S X R X C X D X P	36	.324	.009		
Total	319	14.315			

Table 3

ANOVA of percentage correct on negative trials (EXPERIMENT 1)

<u>SV</u>	<u>df</u>	<u>SS</u>	<u>MS</u>	<u>F</u>	<u>SIG</u>
SUBJECTS (S)	4	18636.64	4659.16		
Runs (R)	1	365.51	365.51		
S X R	4	323.02	80.75	4.53	NS
Background (B)	1	2761.25	2761.25		
S X B	4	27434.97	6858.74	.40	NS
Distance (D)	3	5032.51	1677.50		
S X D	12	8566.71	713.89	2.53	NS
Position (P)	3	3831.44	1277.15		
S X P	12	2194.78	182.90	6.98	p < .01
R X B	1	2.45	2.45	.01	NS
R X D	3	359.86	119.95	.73	NS
B X D	3	2215.98	738.66	.01	NS
R X P	3	2179.64	726.55	1.63	NS
B X P	3	1052.15	350.72	.93	NS
D X P	9	6528.14	725.35	2.22	p < .05
R X B X D	3	319.53	106.51	.34	NS
R X B X P	3	848.95	282.98	2.63	NS
R X D X P	9	2485.40	276.15	2.00	NS
B X D X P	9	3814.43	423.83	1.44	NS
S X R X B	4	996.89	249.22		
S X R X D	12	1967.48	163.96		
S X B X D	12	4292.68	357.72		
S X B X P	12	4545.01	378.75		
S X R X P	12	5347.96	445.66		
S X D X P	36	11773.77	327.05		
S X R X B X D	12	3799.01	316.58		
S X R X B X P	12	1292.33	107.69		
S X R X D X P	36	4970.64	138.07		
S X B X D X P	36	10616.04	294.89		
R X B X D X P	9	2239.08	248.79	.95	NS
S X R X B X D X P	36	9441.27	262.26		
Total	319	150235.52			

Table 4

ANOVA of response speed on negative trials (EXPERIMENT 1)

<u>SV</u>	<u>df</u>	<u>SS</u>	<u>MS</u>	<u>F</u>	<u>SIG</u>
SUBJECTS (S)	4	1.0839	.2710		
Runs (R)	1	.0077	.0077	.89	NS
S X R	4	.0347	.0087		
Background (B)	1	.0119	.0119	1.45	NS
S X B	4	.0330	.0082		
Distance (D)	3	.0388	.0129	2.30	NS
S X D	12	.0672	.0056		
Position (P)	3	.0814	.0271	6.16	p < .01
S X P	12	.0534	.0044		
R X B	1	.0206	.0206	1.93	NS
R X D	3	.0398	.0133	1.12	NS
B X D	3	.0493	.0614	8.20	p < .005
R X P	3	.0352	.0117	1.17	NS
B X P	3	.0272	.0091	1.44	NS
D X P	9	.0710	.0079	1.16	NS
R X B X D	3	.0381	.0127	1.74	NS
R X B X P	3	.0269	.0090	2.57	NS
R X D X P	9	.1545	.0172		
B X D X P	9	.0917	.0102	2.22	NS
S X R X B	4	.0426	.0107		
S X R X D	12	.1433	.0119		
S X B X D	12	.0245	.0020		
S X B X P	12	.0760	.0063		
S X R X P	12	.1198	.0100		
S X D X P	36	.2456	.0068		
S X R X B X D	12	.0877	.0073		
S X R X B X P	12	.0415	.0035		
S X R X D X P	36	.3038	.0084		
S X B X D X P	36	.1672	.0046		
R X B X D X P	9	.1594	.0177	2.53	NS
S X R X B X D X P	36	.2506	.0070		
Total	319	3.6283			

Table 5

ANOVA of percentage correct on positive trials (EXPERIMENT 2)

<u>SV</u>	<u>df</u>	<u>SS</u>	<u>MS</u>	<u>F</u>	<u>SIG</u>
SUBJECTS (S)	4	11355.47	2838.87		
Runs (R)	1	1220.70	1220.70	5.81	NS
S X R	4	839.84	209.96		
Crypticity (C)	1	19923.83	19923.83	7.62	NS
S X C	4	10457.03	2614.26		
Distance (D)	3	13177.03	4392.58	7.80	p < .005
S X D	12	6753.90	562.83		
Position (P)	3	365.23	121.74	.28	NS
S X P	12	5269.53	439.13		
R X C	1	2392.58	2392.58	19.60	p < .025
R X D	3	474.61	158.20	1.86	NS
C X D	3	1146.48	382.16	.95	NS
R X P	3	2505.86	835.29	4.57	NS
C X P	3	583.98	194.66	.93	NS
D X P	9	4564.45	507.16	3.08	p < .025
R X C X D	3	2396.48	798.83	10.27	p < .005
R X C X P	3	802.73	267.58	.47	NS
R X D X P	9	4330.08	481.12	1.23	NS
C X D X P	9	3001.95	333.55	1.30	NS
S X R X D	4	488.28	122.07		
S X R X D	12	1019.53	84.96		
S X C X D	12	4839.84	403.32		
S X R X P	12	2191.41	182.62		
S X D X P	36	5933.59	164.82		
S X C X P	12	2511.72	209.31		
S X R X C X D	12	933.59	77.80		
S X R X C X P	12	6824.22	568.68		
S X R X D X P	36	14136.72	392.69		
S X C X D X P	36	9253.91	257.05		
R X C X D X P	9	4064.45	451.61	1.52	NS
S X R X C X D X P	36	10691.41	296.98		
Total	319	154451.13			

Table 6

ANOVA of response speed on positive trials (EXPERIMENT 2)

<u>SV</u>	<u>df</u>	<u>SS</u>	<u>MS</u>	<u>F</u>	<u>SIG</u>
SUBJECTS (S)	4	5.286	1.322		
Runs (R)	1	.031	.031	3.60	NS
S X R	4	.034	.009		
Crypticity (C)	1	.319	.319	1.58	NS
S X C	4	.809	.202		
Distance (D)	3	.062	.021	.98	NS
S X D	12	.255	.021		
Position (P)	3	.038	.013	.81	NS
S X P	12	.188	.016		
R X C	1	.011	.011	.62	NS
R X D	3	.075	.025	3.54	p < .05
C X D	3	.129	.043	2.77	NS
R X P	3	.073	.024	1.92	NS
C X P	3	.064	.021	1.64	NS
D X P	9	.359	.040	2.32	p < .05
R X C X D	3	.071	.024	3.43	NS
R X C X P	3	.026	.009	.61	NS
R X D X P	9	.291	.032	2.11	NS
C X D X P	9	.310	.034	3.19	p < .01
S X R X C	4	.073	.018		
S X R X D	12	.085	.007		
S X C X D	12	.186	.016		
S X R X P	12	.151	.013		
S X D X P	36	.619	.017		
S X C X P	12	.155	.013		
S X R X C X D	12	.082	.007		
S X R X C X P	12	.168	.014		
S X R X D X P	36	.552	.015		
S X C X D X P	36	.388	.011		
R X C X D X P	9	.128	.014	.90	NS
S X R X C X D X P	36	.567	.016		
Total	319	11.585			

Table 7

ANOVA of percentage correct on negative trials (EXPERIMENT 2)

<u>SV</u>	<u>df</u>	<u>SS</u>	<u>MS</u>	<u>F</u>	<u>SIG</u>
SUBJECTS (S)	4	16057.53	4014.38		
Runs (R)	1	1256.11	1256.11	2.23	NS
S X R	4	2248.29	562.07		
Background (B)	1	14661.11	14661.11	2.37	NS
S X B	4	24710.29	6177.57		
Distance (D)	3	506.73	168.91	.18	NS
S X D	12	11484.74	957.06		
Position (P)	3	14594.08	4864.69	6.08	p < .01
S X P	12	9595.39	799.61		
R X B	1	1051.25	1051.25	3.23	NS
R X D	3	2517.61	839.20	6.25	p < .01
B X D	3	4218.21	1406.07	1.35	NS
R X P	3	483.06	161.02	.41	NS
B X P	3	4192.36	1397.45	1.62	NS
D X P	9	5031.20	559.02	3.24	p < .01
R X B X D	3	2055.48	685.16	1.76	NS
R X B X P	3	723.63	241.21	.72	NS
R X D X P	9	7250.01	805.56	3.63	p < .005
B X D X P	9	2386.51	265.17	1.21	NS
S X R X B	4	1302.53	325.63		
S X R X D	12	1612.23	134.35		
S X B X D	12	12525.38	1043.78		
S X B X P	12	10340.98	861.75		
S X R X P	12	4752.78	396.07		
S X D X P	36	6214.33	172.62		
S X R X B X D	12	4675.49	389.62		
S X R X B X P	12	4045.59	337.13		
S X R X D X P	36	7981.89	221.72		
S X B X D X P	36	7902.14	219.50		
R X B X D X P	9	4690.85	521.21	1.16	NS
S X R X B X D X P	36	16205.18	450.14		
Total	319	207272.96			

Table 8

ANOVA of response speed on negative trials (EXPERIMENT 2)

<u>SV</u>	<u>df</u>	<u>SS</u>	<u>MS</u>	<u>F</u>	<u>SIG</u>
SUBJECTS (S)	4	.4736	.1184		
Runs (R)	1	.0019	.0019	1.5	NS
S X R	4	.0513	.0128		
Background (B)	1	.0263	.0263	1.07	NS
S X B	4	.0983	.0246		
Distance (D)	3	.0540	.0180	1.82	NS
S X D	12	.1191	.0099		
Position (P)	3	.0453	.0151	2.25	NS
S X P	12	.0809	.0067		
R X B	1	.0419	.0419	2.46	NS
R X D	3	.0072	.0024	.34	NS
B X D	3	.0179	.0060	.54	NS
R X P	3	.0154	.0051	1.50	NS
B X P	3	.0045	.0015	.29	NS
D X P	9	.0715	.0079	1.18	NS
R X B X D	3	.0450	.0150	2.17	NS
R X B X P	3	.0023	.0008	.25	NS
R X D X P	9	.1334	.0148	2.31	NS
B X D X P	9	.0976	.0108	1.48	NS
S X R X B	4	.0679	.0170		
S X R X D	12	.0849	.0071		
S X B X D	12	.1327	.0111		
S X B X P	12	.0625	.0052		
S X R X P	12	.0412	.0034		
S X D X P	36	.2416	.0067		
S X R X B X D	12	.0822	.0069		
S X R X B X P	12	.0380	.0032		
S X R X D X P	36	.2307	.0064		
S X B X D X P	36	.2642	.0073		
R X B X D X P	9	.0833	.0093	2.16	NS
S X R X B X D X P	36	.1531	.0043		
Total	319	2.8697			

Table 9

ANOVA of percentage correct on positive trials (EXPERIMENT 3)

<u>SV</u>	<u>df</u>	<u>SS</u>	<u>MS</u>	<u>F</u>	<u>SIG</u>
SUBJECTS (S)	4	2515.63	628.91		
Condition (C)	2	8973.96	4486.98	7.68	p < .025
S X C	8	4671.88	583.98		
Distance (D)	3	9757.81	3252.60	11.91	p < .001
S X D	12	3276.04	273.00		
Position (P)	3	5486.98	1828.99	11.42	p < .001
S X P	12	1921.88	160.16		
C X D	6	2296.88	382.81	1.61	NS
C X P	6	6192.71	1031.12	4.44	p < .005
D X P	9	3356.77	372.98	1.67	NS
C X D X P	18	3369.79	187.21	.76	NS
S X C X D	24	5723.96	238.50		
S X C X P	24	5578.13	232.42		
S X D X P	36	8036.46	223.24		
S X C X D X P	72	17776.04	246.89		
Total	239	88934.92			

Table 10

ANOVA of response speed on positive trials (EXPERIMENT 3)

<u>SV</u>	<u>df</u>	<u>SS</u>	<u>MS</u>	<u>F</u>	<u>SIG</u>
SUBJECTS (S)	4	7.310	1.828		
Condition (C)	2	.074	.037	1.48	NS
S X C	8	.197	.025		
Distance (D)	3	.452	.151	4.31	p < .05
S X D	12	.424	.035		
Position (P)	3	.044	.015	.47	NS
S X P	12	.388	.032		
C X D	6	.147	.024	1.41	NS
C X P	6	.044	.007	.78	NS
D X P	9	.187	.021	1.62	NS
C X D X P	18	.238	.013	1.30	NS
S X C X D	24	.413	.017		
S X C X P	24	.203	.009		
S X D X P	36	.456	.013		
S X C X D X P	72	.743	.010		
Total	239	11.325			

Table 11

ANOVA of percentage correct on negative trials (EXPERIMENT 3)

<u>SV</u>	<u>df</u>	<u>SS</u>	<u>MS</u>	<u>F</u>	<u>SIG</u>
SUBJECTS (S)	4	2015.63	503.91		
Condition (C)	2	5583.33	2791.67	17.60	p < .005
S X C	8	1265.63	158.20		
Distance (D)	3	5895.83	1965.28	10.96	p < .001
S X D	12	2151.04	179.25		
Position (P)	3	13437.50	4479.17	13.15	p < .001
S X P	12	4088.54	340.71		
C X D	6	729.17	121.53	.99	NS
C X P	6	5187.50	864.58	3.04	p < .025
D X P	9	1541.67	171.30	.59	NS
C X D X P	18	4083.33	226.85	1.00	NS
S X C X D	24	2942.71	122.61		
S X C X P	24	6817.71	284.07		
S X D X P	36	10411.46	289.21		
S X C X D X P	72	16307.29	226.49		
Total	239	83458.34			

Table 12

ANOVA of response speed on negative trials (EXPERIMENT 3)

<u>SV</u>	<u>df</u>	<u>SS</u>	<u>MS</u>	<u>F</u>	<u>SIG</u>
SUBJECTS (S)	4	1.303	.326		
Condition (C)	2	.096	.048	4.80	p < .05
S X C	8	.079	.101		
Distance (D)	3	.115	.038	2.11	NS
S X D	12	.219	.018		
Position (P)	3	.113	.038	2.00	NS
S X P	12	.224	.019		
C X D	6	.123	.021	2.33	NS
C X P	6	.132	.022	2.20	NS
D X P	9	.054	.006	1.00	NS
C X D X P	18	.210	.012	2.00	NS
S X C X D	24	.098	.009		
S X C X P	24	.247	.010		
S X D X P	36	.216	.006		
S X C X D X P	72	.411	.006		
Total	239	3.640			

Table 13

ANOVA of percentage correct on positive trials (EXPERIMENT 4)

<u>SV</u>	<u>df</u>	<u>SS</u>	<u>MS</u>	<u>F</u>	<u>SIG</u>
SUBJECTS (S)	4	6864.58	1716.15		
Condition (C)	2	1255.21	627.60	3.58	NS
S X C	8	1401.04	175.13		
Distance (D)	3	2302.08	767.36	5.57	p < .025
S X D	12	4052.08	137.67		
Position (P)	3	12468.75	4156.25	11.88	p < .001
S X P	12	4197.92	349.83		
C X D	6	1119.79	186.63	.43	NS
C X P	6	4140.63	690.10	1.83	NS
D X P	9	2385.42	265.05	.86	NS
C X D X P	18	5567.71	309.32	.85	NS
S X C X D	24	10494.79	437.28		
S X C X P	24	9036.46	376.52		
S X D X P	36	11052.08	307.00		
S X C X D X P	72	26151.04	363.21		
Total	239	102489.58			

Table 14

ANOVA of response speed on positive trials (EXPERIMENT 4)

<u>SV</u>	<u>df</u>	<u>SS</u>	<u>MS</u>	<u>F</u>	<u>SIG</u>
SUBJECTS (S)	4	2.548	.637		
Condition (C)	2	.055	.027	1.93	NS
S X C	8	.109	.014		
Distance (D)	3	.067	.022	.61	NS
S X D	12	.433	.036		
Position (P)	3	.150	.050	2.27	NS
S X P	12	.262	.022		
C X D	6	.046	.008	.53	NS
C X P	6	.125	.021	1.50	NS
D X P	9	.229	.025	1.79	NS
C X D X P	18	.582	.032	1.60	NS
S X C X D	24	.354	.015		
S X C X P	24	.328	.014		
S X D X P	36	.498	.014		
S X C X D X P	72	1.451	.020		
Total	239	7.237			

Table 15

ANOVA of percentage correct on negative trials (EXPERIMENT 4)

<u>SV</u>	<u>df</u>	<u>SS</u>	<u>MS</u>	<u>F</u>	<u>SIG</u>
SUBJECTS (S)	4	1578.13	394.53		
Condition (C)	2	2848.96	1424.48	3.63	NS
S X C	8	1578.13	392.27		
Distance (D)	3	9403.65	3134.55	18.19	p < .001
S X D	12	2067.71	172.31		
Position (P)	3	26028.65	8676.22	18.77	p < .001
S X P	12	5546.88	462.24		
C X D	6	1651.04	275.17	1.64	NS
C X P	6	1463.54	243.92	.72	NS
D X P	9	2752.60	305.85	1.11	NS
C X D X P	18	3036.46	168.69	.57	NS
S X C X D	24	4026.04	167.75		
S X C X P	24	8171.88	340.50		
S X D X P	36	9890.63	274.74		
S X C X D X P	72	21390.63	297.09		
Total	239	101434.93			

Table 16

ANOVA of response speed on negative trials (EXPERIMENT 4)

<u>SV</u>	<u>df</u>	<u>SS</u>	<u>MS</u>	<u>F</u>	<u>SIG</u>
SUBJECTS (S)	4	1.750	.438		
Condition (C)	2	.031	.016	2.23	NS
S X C	8	.060	.007		
Distance (D)	3	.081	.027	2.46	NS
S X D	12	.127	.011		
Position (P)	3	.023	.008	1.14	NS
S X P	12	.080	.007		
C X D	6	.062	.010	2.00	NS
C X P	6	.038	.006	1.20	NS
D X P	9	.030	.003	.43	NS
C X D X P	18	.170	.010	1.43	NS
S X C X D	24	.110	.005		
S X C X P	24	.108	.005		
S X D X P	36	.241	.007		
S X C X D X P	72	.316	.007		
Total	239	3.227			

Table 17

Post-hoc comparisons of percentage correct
on positive slides in Experiment 3
(Dunnett's tests)

Comparison

<u>C. resecta</u> RUNS- NON-RUNS			<u>C. relictata</u> RUNS- NON-RUNS		
Position of <u>Slide</u>	<u>D</u>	<u>SIG</u>	Position of <u>Slide</u>	<u>D</u>	<u>SIG</u>
1-2	.47	NS	1-2	.47	NS
3-4	.16	NS	3-4	.47	NS
5-6	2.16	$p < .05$	5-6	2.03	$p < .05$
7-8	3.59	$p < .005$	7-8	3.47	$p < .005$

Table 18

Post-hoc comparisons of percentage correct
on negative slides in Experiment 3
(Dunnett's tests)

Comparison

C. retecta RUNS-
NON-RUNS

C. relictata RUNS-
NON-RUNS

Position of <u>Slide</u>	<u>D</u>	<u>SIG</u>	Position of <u>Slide</u>	<u>D</u>	<u>SIG</u>
1-2	.77	NS	1-2	.41	NS
3-4	.25	NS	3-4	.95	NS
5-6	1.25	NS	5-6	1.17	NS
7-8	2.11	$p < .05$	7-8	1.87	$p < .05$
	df=24			df=24	

Appendix B:

Table 1-4: Percentage correct on positive and negative trials for individual subjects
(Experiment 3-4)

Table 1

Percentage correct on positive trials (Experiment 3)

		<u>C. relecta</u> RUNS				
Subject Position	91	11	29	70	15	
1	87.5	87.5	100.0	100.0	62.5	
2	75.0	87.5	62.5	62.5	87.5	
3	62.5	87.5	75.0	62.5	62.5	
4	75.0	100.0	100.0	87.5	62.5	
5	75.0	100.0	100.0	100.0	62.5	
6	100.0	100.0	100.0	100.0	100.0	
7	100.0	100.0	87.5	100.0	100.0	
8	100.0	100.0	100.0	100.0	100.0	

		<u>C. relecta</u> RUNS				
Subject Position	91	11	29	70	15	
1	100.0	100.0	62.5	87.5	87.5	
2	62.5	100.0	75.0	75.0	62.5	
3	100.0	100.0	37.5	62.5	87.5	
4	75.0	87.5	87.5	75.0	87.5	
5	100.0	100.0	75.0	62.5	100.0	
6	100.0	100.0	87.5	100.0	100.0	
7	100.0	100.0	100.0	87.5	100.0	
8	100.0	100.0	100.0	100.0	100.0	

		NON-RUNS				
Subject Position	91	11	29	70	15	
1	62.5	100.0	100.0	75.0	87.5	
2	87.5	75.0	62.5	75.0	50.0	
3	75.0	75.0	75.0	87.5	87.5	
4	75.0	62.5	87.5	75.0	62.5	
5	62.5	62.5	100.0	75.0	87.5	
6	62.5	100.0	37.5	87.5	87.5	
7	100.0	75.0	62.5	75.0	87.5	
8	37.5	62.5	87.5	50.0	62.5	

Table 2
 Percentage correct on negative trials (Experiment 3)

		<u>C. resecta</u> RUNS				
Subject Position	91	11	29	70	15	
1	75.0	87.5	87.5	87.5	75.0	
2	75.0	100.0	100.0	62.5	87.5	
3	62.5	62.5	75.0	75.0	50.0	
4	87.5	62.5	100.0	75.0	75.0	
5	75.0	100.0	100.0	100.0	87.5	
6	87.5	87.5	100.0	100.0	100.0	
7	100.0	100.0	100.0	100.0	100.0	
8	100.0	100.0	100.0	100.0	100.0	

		<u>C. relicta</u> RUNS				
Subject Position	91	11	29	70	15	
1	75.0	87.5	62.5	87.5	75.0	
2	25.0	62.5	87.5	87.5	62.5	
3	75.0	75.0	87.5	100.0	75.0	
4	75.0	62.5	87.5	75.0	75.0	
5	100.0	87.5	87.5	87.5	87.5	
6	100.0	100.0	87.5	87.5	100.0	
7	100.0	100.0	87.5	87.5	100.0	
8	100.0	100.0	100.0	100.0	100.0	

		NON-RUNS				
Subject Position	91	11	29	70	15	
1	75.0	100.0	75.0	87.5	62.5	
2	62.5	75.0	87.5	62.5	87.5	
3	50.0	87.5	75.0	87.5	62.5	
4	62.5	87.5	75.0	50.0	62.5	
5	75.0	75.0	87.5	100.0	62.5	
6	87.5	75.0	62.5	75.0	100.0	
7	100.0	75.0	75.0	100.0	62.5	
8	75.0	75.0	75.0	75.0	62.5	

Table 3

Percentage correct on positive trials (Experiment 4)

		<u>C. resecta</u> RUNS				
Subject Position	91	11	29	70	15	
1	75.0	87.5	50.0	87.5	87.5	
2	75.0	87.5	62.5	87.5	87.5	
3	75.0	87.5	100.0	75.0	62.5	
4	62.5	100.0	75.0	100.0	62.5	
5	50.0	100.0	50.0	75.0	100.0	
6	100.0	100.0	100.0	100.0	75.0	
7	100.0	100.0	87.5	100.0	100.0	
8	100.0	100.0	87.5	87.5	100.0	

		<u>C. cara</u> RUNS				
Subject Position	91	11	29	70	15	
1	50.0	75.0	62.5	87.5	100.0	
2	75.0	37.5	87.5	75.0	50.0	
3	75.0	100.0	75.0	87.5	75.0	
4	75.0	100.0	50.0	62.5	100.0	
5	100.0	100.0	87.5	87.5	100.0	
6	100.0	100.0	100.0	100.0	75.0	
7	100.0	100.0	100.0	87.5	87.5	
8	100.0	100.0	87.5	100.0	100.0	

		NON-RUNS				
Subject Position	91	11	29	70	15	
1	75.0	87.5	75.0	75.0	75.0	
2	100.0	100.0	62.5	87.5	62.5	
3	37.5	87.5	62.5	75.0	75.0	
4	62.5	87.5	62.5	62.5	87.5	
5	75.0	100.0	75.0	87.5	87.5	
6	87.5	100.0	87.5	87.5	75.0	
7	87.5	100.0	75.0	87.5	87.5	
8	100.0	87.5	75.0	75.0	75.0	

Table 4
 Percentage correct on negative trials (Experiment 4)

<u>C. resecta</u> RUNS					
Subject Position	91	11	29	70	15
1	87.5	87.5	62.5	75.0	87.5
2	100.0	62.5	62.5	62.5	75.0
3	100.0	75.0	75.0	87.0	75.0
4	100.0	75.0	75.0	62.5	50.0
5	87.5	100.0	87.5	100.0	87.5
6	87.5	100.0	100.0	100.0	87.5
7	100.0	100.0	100.0	100.0	100.0
8	87.5	100.0	87.5	100.0	100.0

<u>C. cara</u> RUNS					
Subject Position	91	11	29	70	15
1	87.5	87.5	87.5	87.5	75.0
2	87.5	62.5	87.5	75.0	25.0
3	50.0	62.5	75.0	75.0	62.5
4	62.5	75.0	50.0	75.0	87.5
5	62.5	75.0	62.5	87.5	62.5
6	100.0	100.0	100.0	100.0	100.0
7	87.5	100.0	100.0	100.0	100.0
8	100.0	100.0	100.0	100.0	100.0

NON-RUNS					
Subject Position	91	11	29	70	15
1	100.0	75.0	87.5	62.5	75.0
2	75.0	50.0	50.0	75.0	75.0
3	50.0	75.0	75.0	62.5	62.5
4	75.0	37.5	62.5	75.0	50.0
5	87.5	100.0	75.0	75.0	87.5
6	75.0	100.0	87.5	100.0	75.0
7	62.5	100.0	75.0	100.0	100.0
8	100.0	100.0	75.0	100.0	87.5

