1986

The effect of crypticity on the foraging efficiency of the blue jay (Cyanocitta cristata).

Deborah Jean Olson
University of Massachusetts Amherst

THE EFFECT OF CRYPTICITY ON THE FORAGING EFFICIENCY

OF THE BLUE JAY (Cyanocitta cristata)

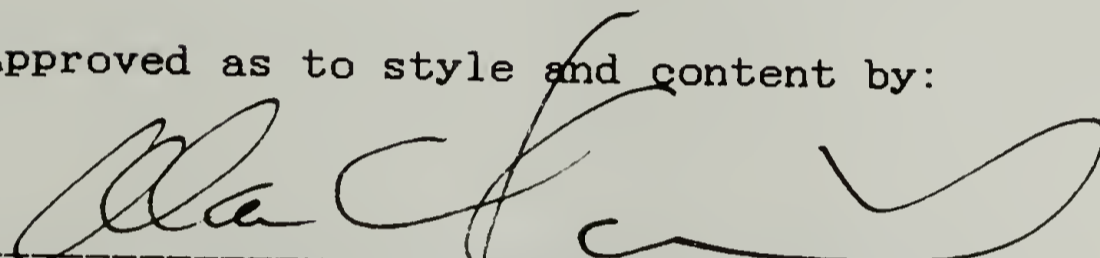A Thesis Presented

By

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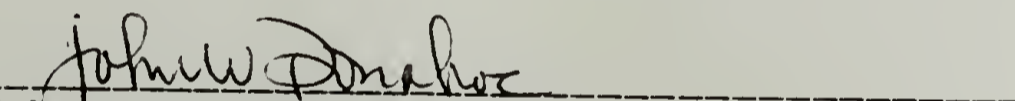OF THE BLUE JAY (Cyanocitta cristata)
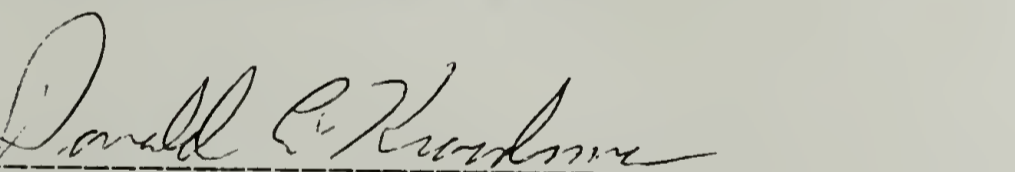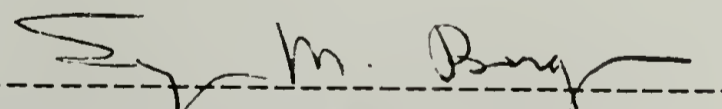
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ACKNOWLEDGEMENTS

ABSTRACT

THE EFFECT OF CRYPTICITY ON THE FORAGING EFFICIENCY

OF THE BLUE JAY (Cyanocitta cristata)

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The present experiment investigated the effect of
crypticity on the foraging efficiency of the blue jay
(Cyanocitta cristata). Four blue jays trained to search
slides for cryptic prey served as subjects. The slides
showed a white birch tree (Betula papyrifera) which
sometimes contained a Catocola relicta moth resting on the
tree. Two response manipulanda were available for the jays
to use when viewing the slides. Responses made to one
alternative always turned the slide off and were not
reinforced. Responses made to the other alternative
initiated a 30 sec interval and eliminated the alternative
for turning the slide off. The first response made after
the interval turned off the slide and produced
reinforcement, if a moth had been on the slide. Three white
birch trees were used to vary crypticity. The efficiency of
the jays was determined by manipulating the time available
to search the slides (viewing time). Two predicitons were
made. First, as crypticity increases, foraging efficiency

(number of prey taken per minute) should decrease. Cryptic prey require longer search times to correctly identify them and fewer prey are located. The second prediction addressed whether the jays were maximizing foraging efficiency. If the jays were maximizing foraging efficiency at long viewing times, then predictions about changes in the behavior of the jays when the viewing time was reduced can be made. If no differences were observed between the predicted and obtained results, the jays would have shown maximum foraging efficiency. The results showed that crypticity did affect foraging efficiency and as crypticity increased, foraging efficiency decreased. Two jays (J5 & J36) were maximizing foraging efficiency and were adjusting their search times based on crypticity. Two jays (J31 & J35) were not maximizing foraging efficiency. These jays were using crypticity and viewing time to adjust their search times.

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INTRODUCTION

The purpose of the proposed research was to determine whether the performance of blue jays (<u>Cyanocitta cristata</u>) searching for <u>Catocola relicta</u> moths was as efficient as possible. Cryptic prey present foraging animals with two characteristics which are assumed to reduce predation (Sargent, 1973, 1978). First is their crypticity. This allows them to be well camouflaged when resting against an appropriate substrate. For example, Sargent (1981) has shown that <u>C. relicta</u> moths have several behavioral tendencies which are used in selecting the appropriate substrate and the optimal resting position. Second, cryptic prey tend to be dispersed (Tinbergen, 1960). These two strategies result in patchily distributed prey, where each patch will contain a maximum of one well camoflauged prey.

Three strategies which predators could use to improve their foraging efficiency in the face of these defenses are: (1) formation of search images (Tinbergen, 1960); (2) adjusting the amount of time spent searching in a patch (marginal value theorem, Charnov, 1976); and (3) varying the search rate depending on the crypticity level of the prey (Gendron & Staddon, 1983).

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Search Image Formation

Tinbergen (1960) postulated that foraging animals (or predators) form a search image for a prey type. As a predator successfully encounters and captures prey of a particular type the search image for that type is strengthened. Use of the search image would increase the probability of the predator correctly identifying the next prey encountered of the same type as a food item. This strategy will improve foraging efficiency by allowing fewer prey to escape.

Croze (1970) using carrion crows (Corvus corone), Pietrewicz & Kamil (1979) using blue jays (C. cristata) and Gendron (unpublished) using bobwhite quail (Colinus virginianus) have shown that these birds are able to form search images for cryptic prey. However, Pietrewicz & Kamil (1979) have shown that for blue jays when the formation of two concurrent search images is required the probability of detection for either prey species is reduced and learning is indicated by a decrease in the latency to respond during acquisition (Pietrewicz, unpublished dissertation).

It would appear that although the formation of search images does increase the detection of cryptic prey when only one prey species is used, it has limited usefulness for multiple prey. It also does not address questions of how long or fast to search for prey.

Marginal Value Theorem

Charnov (1976) proposed an optimal foraging model predicting when a predator should leave a patch. A patch is a discrete area in which the animal is foraging and the environment consists of a number of patches. The resources in a patch are depleted as the foraging bout of the animal continues. At some time the animal will have to leave the patch and travel to a new patch. The marginal value theorem states that a foraging animal should leave a patch when the expected rate of intake in the patch equals the rate of intake for the environment. The model assumes that depletion is occurring in the patch as the forager captures prey, the prey are patchily distributed and the forager has to travel between the patches. One prediction of this model is that as the travel time increases (the amount of time required to move between patches) the time spent in each individual patch will increase. This prediction has been shown to be qualitatively correct (e.g., Krebs, Ryan & Charnov, 1974; Cowie, 1977).

Cryptic prey, however, fit only two of the criteria for the marginal value theorem. Since a patch will contain a maximum of one prey, the assumption made by the model that depletion occurs is violated. Fitzpatrick (1981) suggested that the marginal value theorem could be applied for 0-1 prey situations. Since the prey are in patches of 0

or 1, the longer a predator spends searching a particular patch without encountering a prey, the lower the probability of a prey being present. If the time spent searching is an indicator of whether prey are present, then the 0-1 prey/patch situation is similar to the situation for which the original marginal value theorem was developed. The modified version predicts a predator should leave the patch when the time spent in the patch equals the average time to locate the prey for the environment. This model appears to fit the cryptic prey situation, since the prey are dispersed and would be located in patches of 0 or 1.

Kamil, Lindstrom & Peters (1985) tested the modified version of the marginal value theorem using blue jays searching for cryptic C. relicta moths. They used the laboratory procedure developed by Pietrewicz & Kamil (1979). Blue jays were shown slides of a white birch tree (Betula papyrifera). Some of the slides contained a C. relicta moth located randomly on the tree. They were trained to respond to the slide when a moth was present and to an alternative key when no moth was present. Travel time was varied to test the predictions of the model by manipulating the time before the jays could project the slide. Qualitative support for the Fitzpatrick version of the marginal value theorem was obtained. As the travel time increased the amount of time spent searching the empty

slides increased. However, further analyses showed that quantitatively the marginal value theorem did not hold and the jays were using a more complex strategy, causing them to search longer when no moth was present than predicted. The jays may have been using crypticity, as well as travel time, to adjust their search time. Therefore, even though time in patch is important in determining when to leave, the strategy used by predators is even more complex than this model predicts.

Search Rate

It is possible that crypticity affected the search time of the jays causing the search times for empty slides to be longer than predicted. When the prey are cryptic, they are harder to detect, therefore, it should take longer to locate them. Kamil, Endler & Olson (in prep) tested this hypothesis by varying prey crypticity. The procedure was the same as Kamil et. al (1985). Crypticity was varied by using eight white birch trees. Each tree varied in the amount of black and white present. The easiest tree was almost all white, making the moth quite conspicuous. The other trees included more black and various patterns of black and white. Ten slides were made for each tree. Three slides of each tree contained a C. relicta moth resting on the tree.

Each experimental session included 10 slides of each tree. The blue jays received 48 sessions with these slides. For each trial the latency to respond and whether the response was correct were recorded. Only correct responses to moth slides were reinforced. The results of this experiment indicate that the jays adjusted the amount of time they spent searching the slides depending on the tree. The white tree had the highest percentage correct and shortest latencies to respond for moth and no-moth slides indicating the moths on this tree were highly conspicuous. As the amount of black increased and the pattern of black and white became more complex, the percentage correct decreased and the latencies increased for moth and no-moth slides. The differences in crypticity also were apparent in the moth slides for some trees. For these trees there were differences in percentage correct and latency for the moth slides. This result shows that crypticity level is affected by substrate and the resting position of the prey on the substrate.

Gendron & Staddon (1983) have proposed a model that attempts to predict the search rate of a predator as a function of the crypticity of the prey. The optimal search rate occurs when the rate of prey captured is maximized. The model predicts the optimal search rate will decrease as crypticity increases.

For example, suppose you are the predator and the prey is a set of keys you are searching for. There are two areas in which the keys could be located. In one area the keys would be conspicuous, but in the other area they would be cryptic (i.e., the same color as the background). The model predicts that in order to successfully locate the keys you should search more slowly in the cryptic area than in the conspicuous area. One assumption of the model is that in both areas there is a rate (maximum search rate) at which you will be unable to detect the keys. This maximum search rate will be the same for both areas and for any other person searching for the keys.

The results of the Kamil et. al experiment (in prep) qualitatively support this model. As crypticity increased the jays spent more time searching the slides. Gendron & Staddon (1984) have shown empirically that the predictions of the model are supported when humans are given the task of searching for a target object on various backgrounds. In their experiment human subjects were shown computer generated stimuli projected onto a computer monitor. The subject's task was to search for a target object that may have been located on the background. If the subject detected the target, they were instructed to press a button. Crypticity of the target was varied by changing the background on which the target was presented. The amount of time to view the screen was controlled by the experimenter

and was used as an estimation of search rate. The results of this study indicate that the probability of detecting a prey is related to the crypticity. As the time to view the stimuli decreased, the percentage correct also decreased, but at different rates for the crypticity levels. The more cryptic the target object, the faster the decrease in percentage correct occurred.

Gendron (unpublished) has also shown that bobwhite quail will adjust their search speed depending on the crypticity level of the target object they are searching for. Bobwhite quail were allowed to search for pellets placed in a crushed corncob bedding dyed green. The pellets were colored brown or one of five shades of green. Only one pellet type was present during a trial session. The results of the experiment qualitatively agreed with the predictions of the model. As the crypticity of the pellets increased, the search speed of the quail decreased.

Present Experiment

The present experiment focused on whether blue jays were performing as efficiently as possible for each level of crypticity encountered. The results of the Kamil, Endler & Olson (in prep.) experiment indicated the jays adjusted their search time depending on the level of crypticity. However, this experiment did not provide the data necessary to determine if the jays' behavior results in maximum

efficiency for prey detection. The major problem with the procedure used in their experiment was that there was no method to determine if nondetected moths would have been detected had the jays spent more time searching the slide.

One strategy which might be used to approach this problem would be to use the procedure of Kamil et. al (1985) with two types of sessions. Session type I would be the same as used by Kamil et. al and would allow the jays to respond to two different keys for moth present and no-moth present responses. Session type II would allow the jays to respond to a key for moth present responses, but would eliminate the key for making no-moth present responses. This session type addresses the question of whether all moths will be detected if the jays search longer. The data from session type II could be used to predict what the jays should be doing for session type I. The critical question for the jays' efficiency would be: are the jays responding to no-moth slides (or giving up searching the slide) at the time at which the frequency distribution for latency to respond correctly to moth slides (or attack) is at its maximum. Although this would be an excellent approach to the efficiency question, pilot data show the jays have trouble learning to withhold the no-moth present response. This results in behaviors which are incompatible with continuous search by the jays during session type II.

Another method of addressing the question of efficiency would be to adjust the amount of time available for the jays to search the slide, as in the experiment by Gendron & Staddon (1984). If the viewing time (amount of time available for the jays to search the slides) is initially set high, so all slides could be correctly identified, baseline behavior when the jays control the stimulus duration could be obtained. The viewing time could then be systematically manipulated and predictions about what the birds should do can be made. For example, if the jays are performing as efficiently as possible at long viewing times, then changes in viewing time should affect the percentage of slides which are correctly identifed. The percentage of slides which can no longer be identified should be proportional to the percentage of slides with correct identification times longer than the reduced viewing time. However, if the jays are able to adjust their behavior to include the percentage of slides with latencies longer than the viewing time, this would indicate that the jays are not performing as efficiently as possible.

The present experiment employed the procedure just described. The jays responded to two separate keys during the trial after the stimuli had been presented. The procedure used was the Kamil et. al (in prep) procedure. Three white birch trees varying in the amount and patterning of black and white were used. The viewing time

was manipulated as outlined above. The data were analyzed to determine the efficiency of the jays and were also subjected to the Gendron & Staddon model in an attempt to determine the crypticity levels of the slides used.

CHAPTER II

METHOD

Subjects

Four adult blue jays, three of unknown sex and one
female (J31) served as subjects. All birds were hand reared
in the laboratory and were individually housed on a 13/11
hr. light/dark cycle. All birds received six experimental
sessions per week and were maintained at 80% of their free
feeding weights with controlled feedings. All birds had
previous experience with searching for cryptic prey on
slides and with the slides used in the present experiment.

Apparatus

The experimental chamber was 36.5 cm. x 30.5 cm. x 35
cm. (HxLxW) and was housed in a sound attenuating chamber
42 cm x 56 cm x 37 cm (HxLxW). Masking white noise was
provided by a speaker located behind the intelligence
panel. Ventilation and additional masking noise was
provided by a fan on the rear wall. Reinforcements were
delivered by a Davis Universal Feeder. The food cup was 3.5
cm high, 4.5 cm long and was centrally located on the
intelligence panel, 8.25 cm from the floor. The houselight
was 2.5 cm in diameter and located in the upper right hand
corner of the intelligence panel.

Two keys on the intelligence panel were used for stimulus presentations and response manipulanda. Both keys were located to the left of the food cup. The rectangular key was 7.5 cm high and 11.6 cm long. The center of the key was 9 cm from the left edge of the panel and 21.5 cm from the floor. The round key was 2.5 cm in diameter and the center was 13 cm from the left panel edge and 13 cm from the floor. A perch was 10 cm in front of and ran parallel to the intelligence panel. It was raised 4 cm above the floor so that the rectangular key was approximately at eye level.

Stimuli were projected onto the round key by an IEE projector. A programmable Kodak Carousel projector, Model 650H, was used for rear projection of stimuli onto the rectangular key. A Data General Nova computer and Lehigh Valley Interact system were used to control and record all experimental events. Data from each session were stored on magnetic tape for later analysis.

Slides

The slides were photographed in the field with a Nikon 35 mm camera and a 50 mm Nikkor-H lens at a subject-to-camera distance of 1.6 m. Each slide displayed one white birch tree. Three trees were used. They varied in the amount and patterning of black and white bark. One tree was almost all white (for conspicuous moths), one tree was a

complex pattern of black and white (for cryptic moths) and the third tree was intermediate in the complexity of black and white. Each set (all slides of the same tree) had 64 slides, 16 of which contained a C. relicta moth. The moth was always resting in its species typical position (head-up) and located on a different section of the tree for each slide. Figures 1-3 show examples of moth slides for each set.

Procedure

An experimental session consisted of 64 trials with only one set (tree) shown during each session. Each slide set was shown twice a week and for no more than two consecutive sessions.

A trial began with the projection of a white cross on the round key. Responses made to this key had no effect. After five sec the key color changed to yellow. The first subsequent response to the round key caused a slide to be projected onto the rectangular key and the round key color changed to red. At this time the bird could respond to either of the keys. If the bird did not respond to one of the keys, both keys were darkened after a specified amount of time (called viewing time - see experimental stages for a discussion of the times used.)

A peck at the rectangular key darkened the round key, making it inoperative, and initiated a 30 sec interval. The first peck at the rectangular key after this interval darkened the rectangular key. If a moth was displayed in the slide, the bird received half a _Tenebrio_ larvae and the projector advanced to begin the next trial. If no moth was present, the projector advanced to begin the next trial. A peck at the round key darkened both keys and advanced the projector for the next trial. If the bird had not responded to either of the keys by the end of the viewing time, both keys were darkened and the projector advanced to begin the next trial.

For each trial the slide type (moth or no-moth slide), key responded to and latency to respond after the slide was projected were recorded.

Slide Sequences

Twelve slide sequences of the numbers 1-60 were generated for slide presentations. Each number corresponded with one slide in each set. The order of sequence presentations was randomly assigned with each sequence being presented once every 12 days.

The first four trials of the 64 trial session were to famialarize the birds with the set and were not analyzed. These trials consisted of three no-moth slides and one moth slide. The order of presentation for these slides was

varied daily, but the slides were not numbered. Slide presentations for the last 60 trials were arranged according to the generated sequences and included 45 no-moth slides and 15 moth slides.

The 60 trials were arranged so that within blocks of 20 trials there were five moth slides with a maximum of one occurrence of two consecutive moth slides per block. For the entire session (64 trials) the upper limit of consecutive no-moth slides was set at six with no limit on the number of times this could occur.

Experimental Stages

The time available for the jays to search the projected slide was varied between stages of the experiment. The viewing time remained constant within a stage. The viewing time was changed when the bird showed 5 days of stable response latencies to each set. The stable latency measure used was the median for the slide type (moth or no-moth) that produced the most variable latency data. The median included both correct and aborted trials for the slide type. A trial was correct if the rectangular key was pecked when a moth was present or if the round key was pecked when no moth was present. A response to the opposite key defined as a correct response for the slide type resulted in an incorrect trial. A trial was considered

aborted if there was no response by the end of the viewing time. The latencies for no-moth slides were most variable for J5, J35 and J36. The latencies for moth slides were most variable for J31.

Data from a pilot study using the same jays and slides as the present experiment were used to determine the baseline viewing times (first and last stage). These viewing times were chosen to be long enough to allow the birds to respond on every trial. Table 1 lists the number of stages, the viewing time used for each stage and the number of sessions per stage for each jay.

Reductions in viewing times were determined using the data from the last five days of each viewing time and used only the correct trials for the appropriate slide type. For each slide set frequency distributions were obtained for 0.5 sec blocks and were used to determine the new viewing time. The first viewing time reduction was the time at which approximately 20% of the longest latencies would be eliminated. The jays received a second reduction if the percentage of aborts for the no-moth slides was less than 50%. The second reduction in viewing time was the median latency for the target slide type. After completion of the final viewing time reduction all jays were returned to the first viewing time received.

TABLE 1. Total days and maximum viewing time per condition
for individual jays.

J#	VT1		VT2		VT3		VT4	
	DAYS	SECS	DAYS	SECS	DAYS	SECS	DAYS	SECS
5	27	20.5	24	5.5	21	20.5	--	----
31	24	30.5	24	11.5	24	6.0	21	30.5
35	33	14.5	24	7.5	21	14.5	--	----
36	24	16.5	21	6.5	24	4.0	21	16.5

Figure 1. Representative moth slide used
    in Set 1. The moth is centrally located
    on the tree.

Figure 2. Representative moth slide used
in Set 2. The moth is centrally located
on the tree.

Figure 3. Representative moth slide used
    in Set 3. The moth is centrally located
    on the tree.

C H A P T E R   I I I

RESULTS

Data analysis was done with the IDAP statistical package for APL using the Control Data Corporation NOS software system. Binomial distributions were obtained with the Microstat software package for the North Star microcomputer.

For the purpose of data analysis a trial was considered correct if the bird responded to the rectangular key when a moth was present (moth slide) or to the round key when no moth was present (no-moth slide). If the bird responded to the opposite key defined as correct for that slide, the trial was incorrect. A trial was correct or incorrect only if the bird responded during the viewing time. When no response had been made by the end of the viewing time the trial was termed an aborted trial. Only the last 60 trials of each session were analyzed.

All data analyses were carried out for individual birds. The data analyses addressed several issues. These were: (1) differences between individual slides within a set; (2) effects of the independent variables: viewing time and set; (3) differences between predicted and obtained latencies and percentage aborts; (4) rate of prey capture (number of prey taken/minute search time); and (5) levels of crypticity for each set (Gendron & Staddon model).

Analysis of Slides Within a Set

If each set represents a specific level of crypticity, it is important that the slides for each type (moth and no-moth slides) within each set be relatively homogenous. Average latency measures were obtained for each slide for the last 5 days for both the first and last viewing times. Separate analyses of variance were performed for each slide type within a set for the first and last viewing time for individual birds resulting in 48 analyses. Results of these analyses showed no differences between the latencies for the no-moth slides within a set, all p's > .05. For the moth slides there were a few individual differences in latencies for the sets (4 of the 24 analyses). However, these differences were not consistent between the two stages for an individual bird (J36) or between the different birds. Since there were no consistent differences between the moth slides within a set all further analyses treated the moth slides for a set as a homogenous type.

Effects of Viewing Time and Set

Daily averages for six dependent variables were obtained for the last five days of each stage. The variables were percentage correct for moth or no-moth slides, percentage abort for moth or no-moth slides and the latencies to respond for correct moth trials (attack time,

ATT) and for correct no-moth trials (giving up time, GUT). Percentages were obtained by dividing the number of correct or aborted trials for the slide type by the total trials for that slide type (15 for moth slides and 45 for no-moth slides) and multiplying by 100.

Analysis of variance was performed for each dependent variable (24 analyses). Since there was no set x viewing time interaction present in any of these analyses (all p's > .05) only the main effects are presented.

Three slide sets were used to manipulate prey crypticity. The results of the Kamil, Endler & Olson (in prep.) experiment indicate there should be differences between the slide sets for percentage correct and latency. Moth and no-moth slides for the easiest set should have the highest percentage correct and the shortest latencies. As the crypticity of the slide sets increase, the percentage correct should decrease and the latencies should increase for moth and no-moth slides.

Table 2 shows the F values for the main effect of set differences. The dependent variables for the moth slides show that Set 1 was ranked easiest with the shortest ATT, highest percentage correct and the lowest percentage aborts. Set 3 was ranked hardest with the longest ATT, lowest percentage correct and the highest percentage aborts. Set 2 was ranked intermediate. The only exceptions to this were J31 on ATT, with Set 3 being the easiest,

TABLE 2. F values for the analysis of set differences. Six dependent variables are shown for each jay. Probabilities are shown for significant variables.

J#	POSITIVE			NEGATIVE		
	%COR	%ABT	ATT	%COR	%ABT	GUT
5[a]	3.79[b]	<1	1.22	1.16	1.28	1.20
31[a]	6.28[c]	7.00[c]	6.40[c]	4.42[b]	4.02[b]	7.50[d]
35[a]	16.68[d]	10.31[d]	11.02[d]	1.95	1.09	12.10[d]
36[a]	3.18[b]	1.32	6.95[c]	5.72[c]	5.73[c]	6.63[c]

a. df = 2,36 for J5 & J35 ; df = 2,48 for J31 & J36
b. p < .05 (%COR positive for J36 p = .05)
c. p < .01
d. p < .001 (GUT for J31 p = .001)

Set 2 the hardest and Set 1 intermediate, and J35 on percentage correct for moth slides with Set 2 being the easiest, Set 1 intermediate and Set 3 the hardest.

The set rankings obtained for the dependent variables for no-moth slides were not as orderly as the moth slides. Different rank orderings were obtained for GUT and percentage correct. Three jays (J31, J35 & J36) showed significant results for GUT. The rank ordering for the sets from shortest to longest latency was: Set 1 easiest, Set 2 intermediate and Set 3 hardest. Two jays (J31 & J36) had significant results for percentage correct. The set ranking from highest to lowest percentage correct was Set 3, Set 2 and Set 1. The rank ordering for percentage aborts for these two jays was the same as percentage correct.

Table 3 summarizes the results of the set rankings. The results show there was a difference in the crypticity of the three slide sets. Set 1 was the easiest (most conspicuous) set. Set 3 was the most cryptic set and Set 2 was intermediate. The only exception was the set rankings for no-moth slides for percentage correct and percentage aborts where Set 3 and Set 1 were reversed. Possible reasons for this unpredicted result are discussed later.

There was a significant main effect of viewing time for all dependent variables (all p's < .05). The results were the same for moth and no-moth slides. When the viewing time was reduced, percentage correct decreased, percentage

TABLE 3. Rank order for each set. Set rankings for
the dependent variables are shown in the matrix
with 1 representing the easiest set and 3 the
hardest set.

		SET #		
		1	2	3
		==========		
MOTH	SLIDES			
	%COR	1	2	3
	%ABT	1	2	3
	ATT	1	2	3
NO-MOTH	SLIDES			
	%COR	2	3	1
	%ABT	2	3	1
	GUT	1	2.5	2.5

abort increased and latencies decreased (see Figures 4-7).
Percentage incorrect was calculated for each viewing time
as 100-(% correct + % abort) for moth and no-moth slides.
There was no diffence between viewing times for this
dependent variable.

Since reductions in viewing time were used to assess
the relative efficiency of the jays at long viewing times,
it is important to know how this manipulation affected
behavior. If the reductions in viewing time cause the jays
to change their search strategy, this procedure would be
inappropriate for the purpose of the present experiment.
Three changes in strategy which might occur would be:
(1) respond to all slides as if they were moth slides;
(2) respond randomly to the slides; and (3) quit responding
to no-moth slides. The first and second strategies would
indicate the jays were no longer searching the slides and
the third strategy would result in uninterpetable results
for no-moth slides.

The analysis of the main effect of viewing time show
that reductions in viewing time did not cause the jays to
change their search strategy. The results for percentage
incorrect show that the jays did not respond randomly when
viewing time was reduced. Since there were few errors at
the longest viewing time, there would have been an increase
in percentage incorrect for moth and no-moth slides. The
jays did not respond to all slides as if they were moth

slides when viewing time was reduced. If they had, percentage correct for moth slides would have been 100%. The results for percentage correct for no-moth slides show the jays did not quit responding to no-moth slides. If this had happened, percentage correct for no-moth slides would have been 0%.

Analysis of Predicted and Obtained Aborts and Latencies

The results of the viewing time analysis show the jays changes in percentage correct and percentage abort were not due to a change in strategy when the viewing time was reduced. The next set of analyses focuses on what effect the viewing time reductions had on the efficiency of the jays. When the viewing time was reduced it was possible to predict what the jays should do, if they had been performing as efficiently as possible. If the results obtained do not differ from the predicted results, the jays were performing as efficiently as possible at the longer viewing time. For moth and no-moth slides the predicted and obtained results were compared for percentage abort and latency. Percentage abort was used, since the longest viewing time was chosen so no aborts would occur.

The percentage predicted aborts for each viewing time reduction was calculated from the last 5 days of the preceding viewing time. For each slide type/set the

predicted percentage was the percentage of trials responded to past the newly calculated viewing time plus the percentage aborts for the preceding viewing time. For example, if the viewing time was 20 sec., the number of trials responded to were calculated for blocks of seconds. An example would be:

LATENCY	#TRIALS
0 - 9.9	10
10 - 19.9	3
20	2

If the viewing time was reduced to 10 sec., the predicted percentage abort would be $((2+3)/15)*100$ or 33%. The predicted aborts for the first viewing time were assumed to be zero and for the last viewing time the value obtained in the first viewing time was used, since these two viewing times were the same.

The predicted latency was calculated for each slide type/set. It was the average latency of the correct trials from 0 sec. up to but not including the new viewing time. This was not calculated for the first and last viewing times. Figures 4-7 show the predicted values for each bird for individual sets.

Binomial distributions were obtained for each slide type/set based on the percentage predicted aborts and the total number of trials for each slide type (75 trials for moth slides and 225 trials for no-moth slides). The criterion was set at alpha = .05 for a two-tailed test. The

binomial was chosen rather than a t since exact probabilities could be used. Analysis of variance was used to test for differences between predicted and obtained latencies for each viewing time reduction.

Since the percentage of predicted aborts was generally equal to or close to zero for the first and last viewing times this analysis is not of much interest (only a few aborts needed to occur to make the results significant). However, when the viewing time was reduced, the comparison of percentage predicted and obtained aborts show that the jays responded differently to the viewing time reduction on the moth and no-moth slides. The jays significantly decreased their responding on the no-moth slides, which resulted in more aborts than predicted. (The only exception to this was J31. This bird made less aborts than predicted for Set 3 for both viewing time reductions and also for Set 1 during the second viewing time reduction.)

All of the jays continued to respond to the moth slides and tended to make less aborts than predicted for Set 1 and Set 3 and made as many aborts as predicted for Set 2 for the first viewing time reduction. For the second viewing time reduction, J31 made less aborts than predicted for all sets and J36 made as many aborts as predicted for Set 1 and Set 2 and more aborts than predicted for Set 3.

The obtained latencies for J31 and J35 were shorter than the predicted latencies (p's < .05) for moth and noo-moth slides. The one exception to this was the GUT for J31 for the first viewing time reduction. In this case there was no difference between the predicted and obtained GUT's. J36 generally did not show any differences between the predicted and obtained latencies for moth or no-moth slides. The one exception for this bird was a shorter GUT than predicted for Set 1 for the first viewing time reduction. J5 did not show any difference for ATT, but the GUT's for this bird were longer than predicted for all sets.

Two conclusions can be drawn from these analyses. First, the jays showed a greater increase in aborts for no-moth slides than moth slides. Possible reasons for this are discussed later. Second, for the moth slides, only two jays (J5 & J36) were performing efficiently at long viewing times. For these jays there was no difference between predicted and obtained values for percentage abort and ATT. J31 & J35 showed decreases in percentage abort by responding sooner, indicating that at long viewing times they were not as efficient as possible.

Rate of Prey Capture

Another method which can be used to determine the efficiency of the jays is to calculate the rate of prey capture for each set and viewing time used. The measure of rate of prey capture used in the present analysis was the number of prey found per minute of search time. If the results of previous analyses were correct, two predictions can be made. First, if crypticity had an effect on rate of prey capture, the more cryptic sets should have lower rates of prey capture. This would be due to fewer prey found and longer search times for cryptic sets. Therefore, Set 1 should have the highest rate of prey capture, Set 3 the lowest and Set 2 would be intermediate. Second, if the jays were performing as efficiently as possible, there sould be no difference in rate of prey capture when the viewing time is reduced. This would predict no change in rate of prey capture for J5 & J36, since the predicted and obtained aborts and ATT were equal, and an increase for J31 & J35. The obtained aborts and ATT for moth slides for these two jays were lower than predicted.

Rates of prey capture were calculated for each set and viewing time for individual jays. The last five days of each viewing time were used to calculate the rate of prey capture. The rate of prey capture was calculated as:

(number of prey found)/total search time (min)

Analysis of variance was used to analyze the data for individual jays.

Analysis of the set results show that Set 1 had the highest rate of prey capture, Set 3 had the lowest and Set 2 was intermediate. This was true for all jays except J5. For this jay there was no difference in the rate of prey capture for the sets.

The viewing time results show there was no difference in the rate of prey capture for the first viewing time reduction. The only exception was J35, where there was an increase in rate of prey capture. For the second viewing time reduction there was a decrease in rate of prey capture for J36 and an increase for J31.

Figure 8 shows these results. The analysis of rate of prey capture shows there was an effect of crypticity. Set 1 had the highest rate of prey capture followed by Set 2 and Set 3. This analysis also shows that J5 & J36 were performing efficiently, since no change in rate of prey capture occurred when the viewing time was reduced. Also, J36 showed a decrease in rate of prey capture when the viewing time was reduced the second time. J31 & J35 were not as efficient as they could have been since J35 showed an increase in rate of prey capture when the viewing time was reduced the first time and J31 showed a similar increase for the second viewing time reduction.

Analysis of the Gendron and Staddon Model

The Gendron & Staddon (1983) model makes predictions about the correlation between search rate and crypticity. Assuming the predator is detecting the maximum prey possible in the least time, the model predicts that the optimal search rate will vary as a function of the level of crypticity. As the crypticity decreases (prey become more conspicuous), the optimal search rate will increase. An estimation of the crypticity level can be obtained when the percentage correct is plotted for viewing time. The shape of the resulting curve indicates the crypticity level. If the curve is concave, the prey are conspicuous. As the prey increase in crypticity the curve will become convex. At 0% correct all the crypticity curves should come together.

Only the data for J31 & J36 were subjected to the Gendron & Staddon analysis, since more than one viewing time reduction is required. Figure 9 shows the data plotted as the percentage correct moth and reciprocal (i.e., speed) of 1/viewing time (curves fitted by eye). The most obvious aspect of this graph is that the moth slides used in this experiment were not very cryptic. This is indicated by the concavity of the lines for each set. It does show the difference between the sets and the ranking order previously mentioned. However, there were not enough viewing time reductions used to be able to determine the

exact crypticity level for each set.

Figure 4. The six dependent variables for J5. The solid lines represent the behavior of the jay. The dashed lines represent the predicted percentage abort for the moth and no-moth graphs. For the latency graphs, the open circle represents the predicted attack time and the open triangle represents the predicted giving up time.

SET 1 SET 2 SET 3

MOTH

% COR

% PRED ABT

% ABT

NO-MOTH

LATENCY (SECS)

GUT

ATT

20.5 5.5 20.5   20.5 5.5 20.5   20.5 5.5 20.5

VIEWING TIME (SECS)

Figure 5. The six dependent variables for J31. The
solid lines represent the behavior of the jay. The dashed
lines represent the predicted behavior of the jay. The
dashed lines for the moth and no-moth graphs represent
the predicted percentage abort. For the latency graphs, the
dashed line connected by the open circles shows the
predicted attack time and the dashed line connected by the
open triangles shows the predicted giving up time.

SET 1   SET 2   SET 3

MOTH

% COR

% PRED ABT

% ABT

NO-MOTH

LATENCY (SECS)

ATT

GUT

30.5 11.5 6.0 30.5   30.5 11.5 6.0 30.5   30.5 11.5 6.0 30.5

VIEWING TIME (SECS)

Figure 6. The six dependent variables for J35. The solid lines represent the behavior of the jay. The dashed lines represent the predicted percentage abort for the moth and no-moth graphs. For the latency graphs, the open circle represents the predicted attack time and the open triangle represents the predicted giving up time.
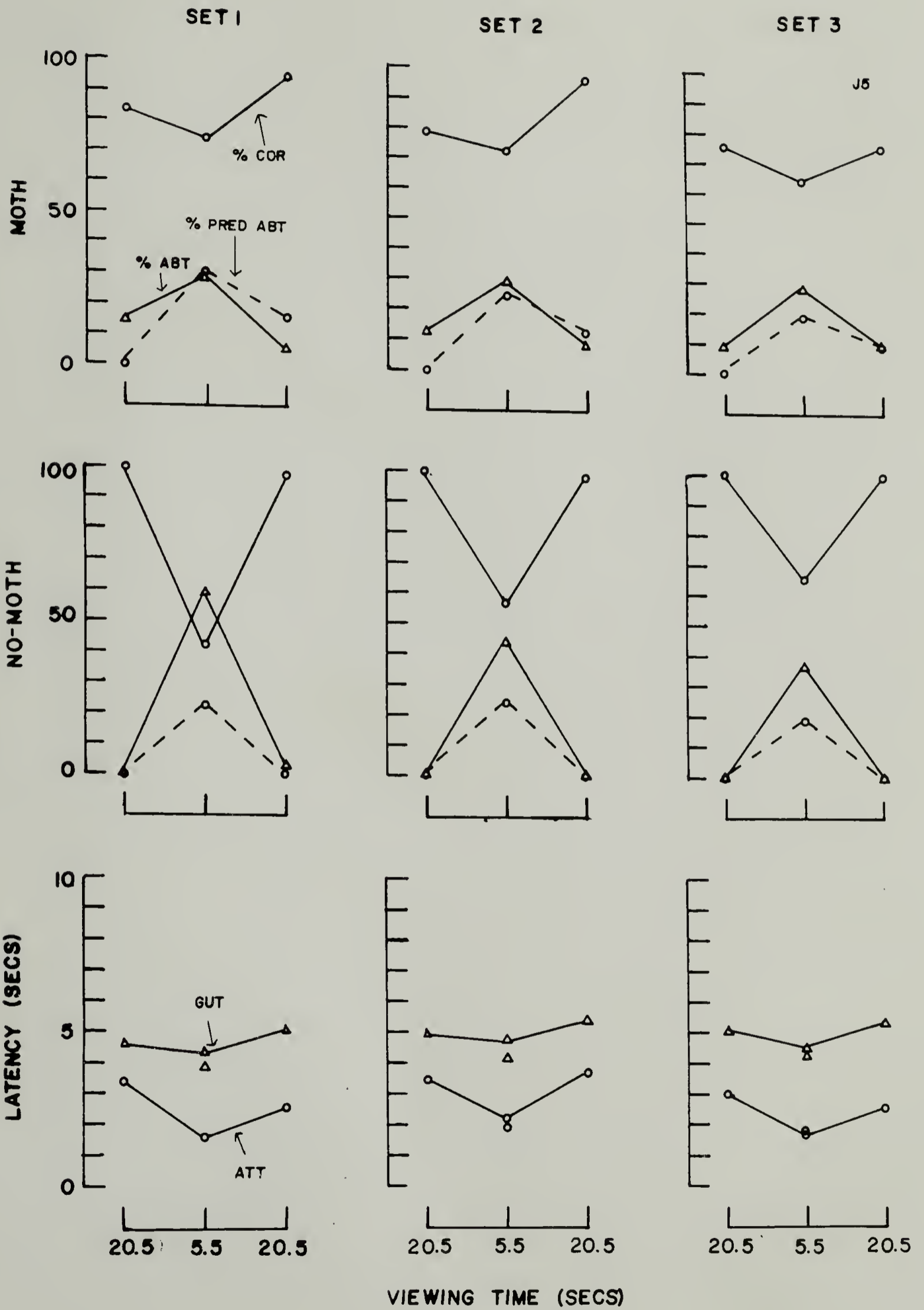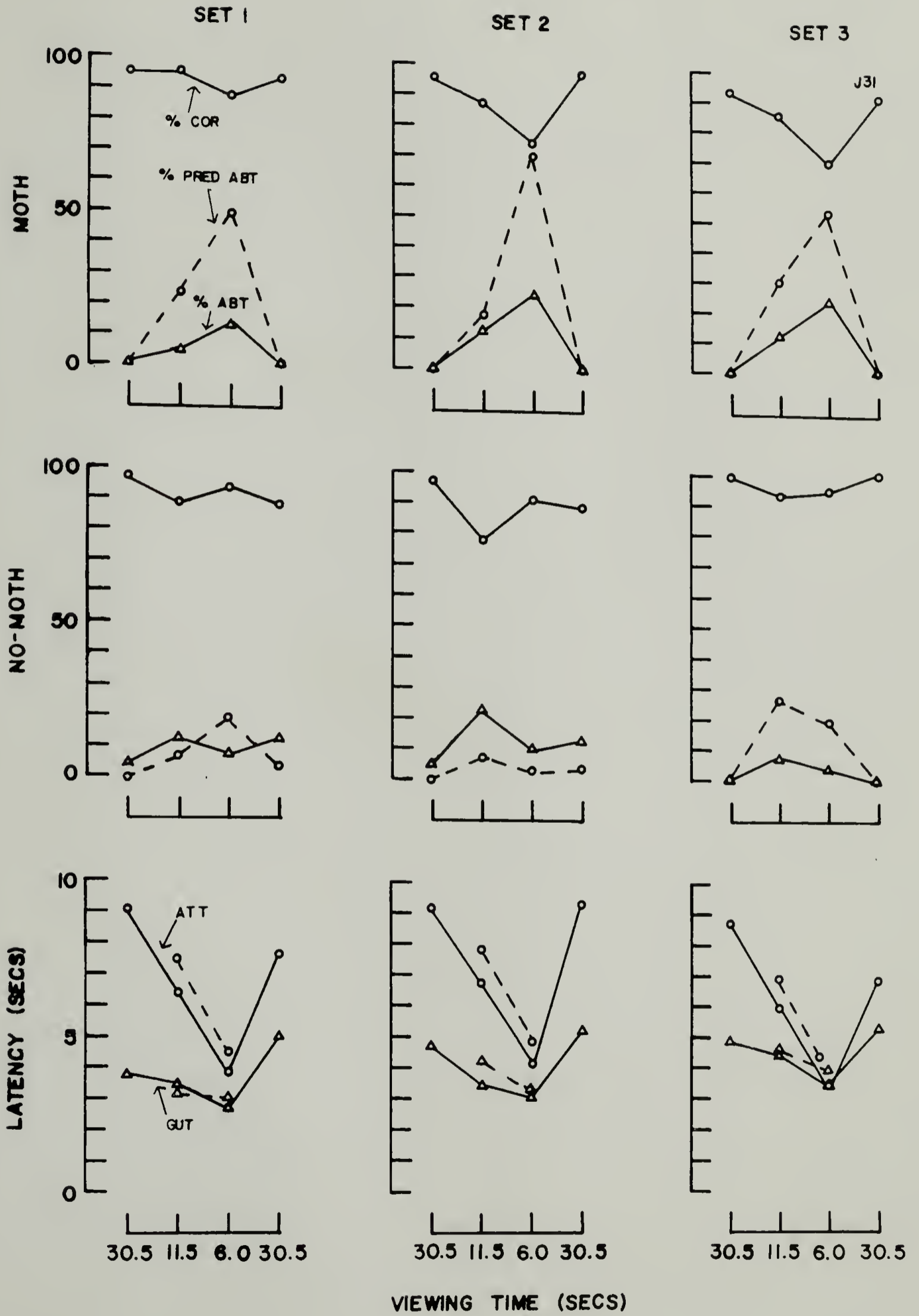
43
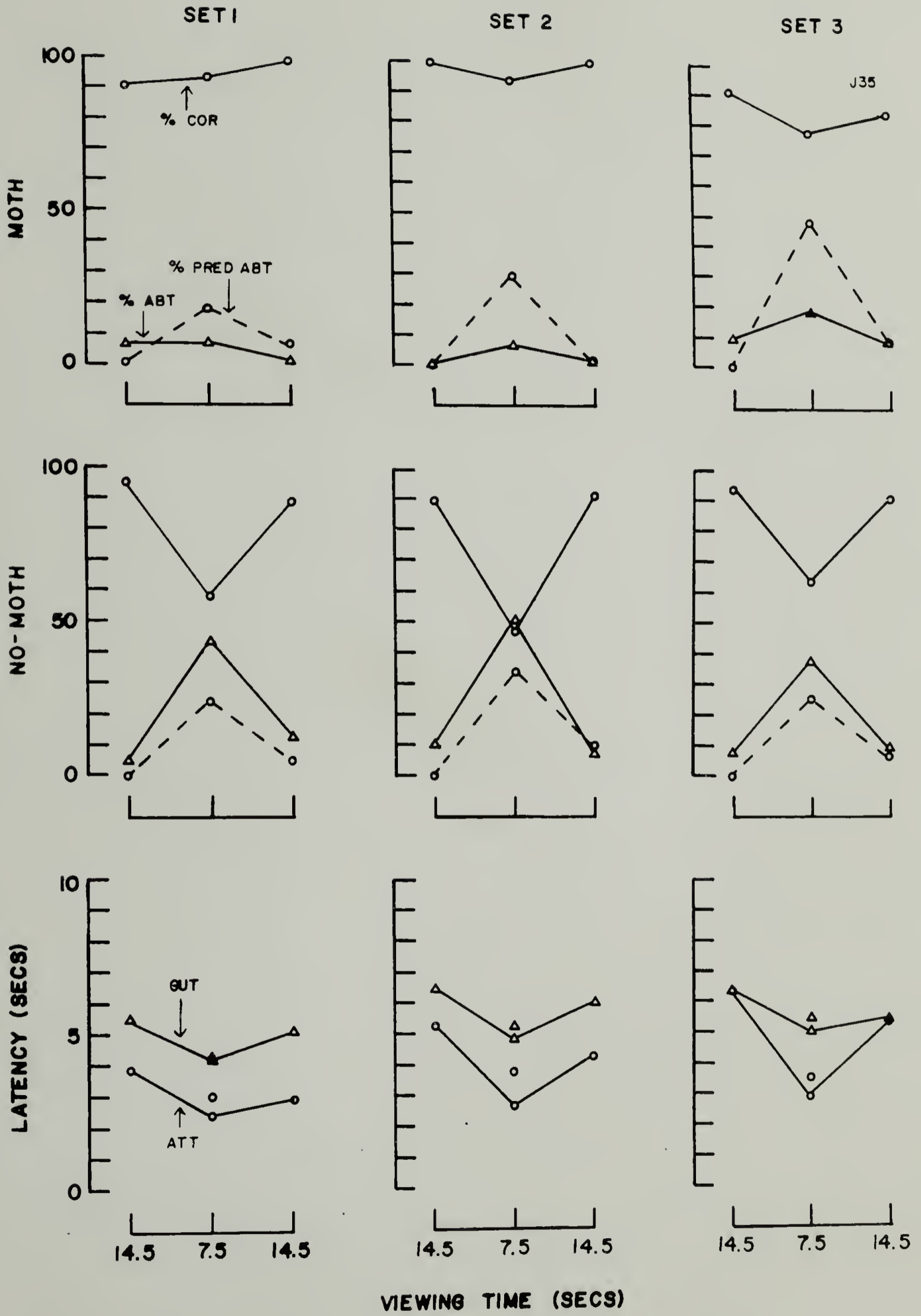
Figure 7. The six dependent variables for J36. The
solid lines represent the behavior of the jay. The dashed
lines represent the predicted behavior of the jay. The
dashed lines for the moth and no-moth graphs represent
the predicted percentage abort. For the latency graphs, the
dashed line connected by the open circles shows the
predicted attack time and the dashed line connected by the
open triangles shows the predicted giving up time.

SET 1   SET 2   SET 3

MOTH

NO-MOTH

LATENCY (SECS)
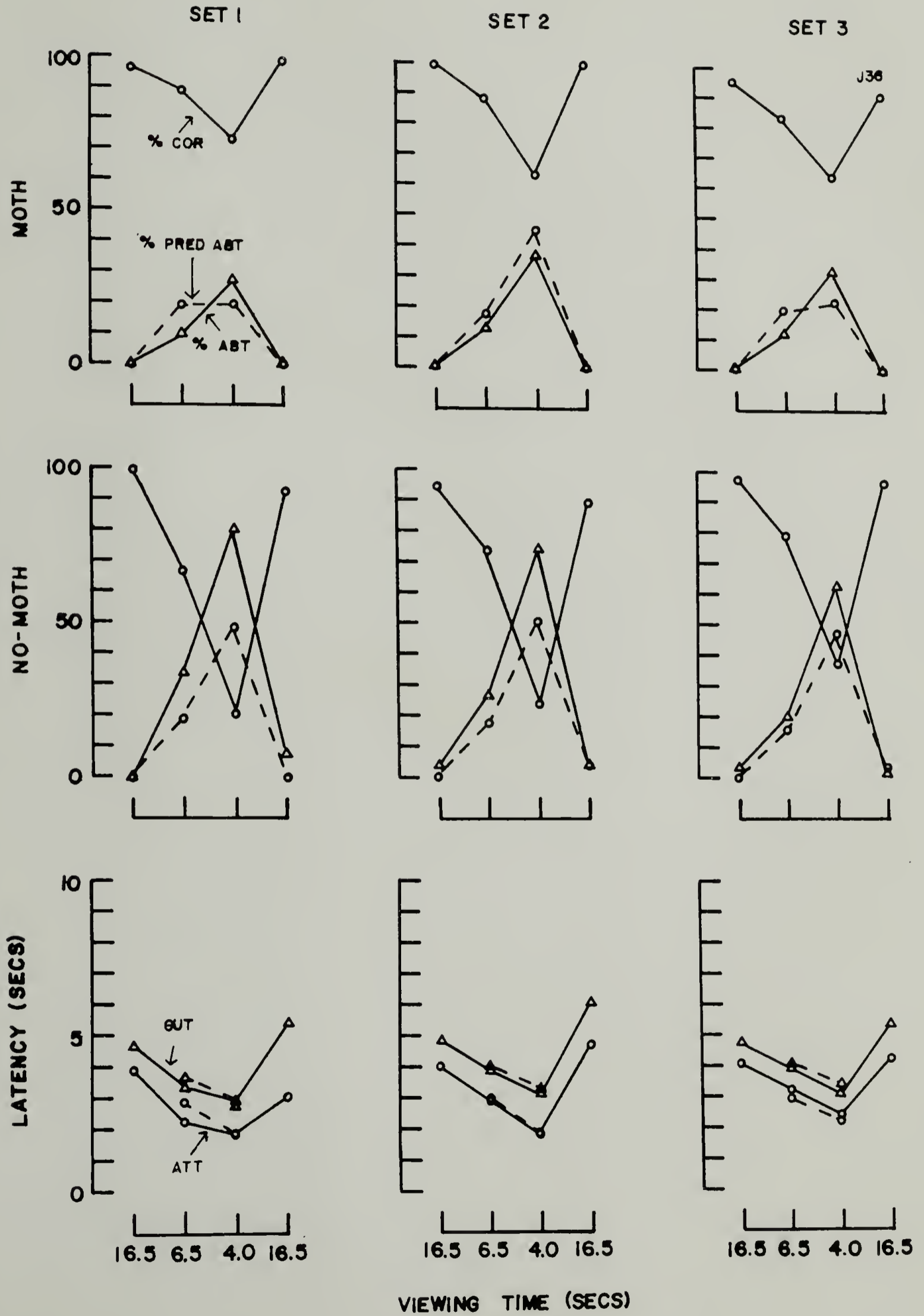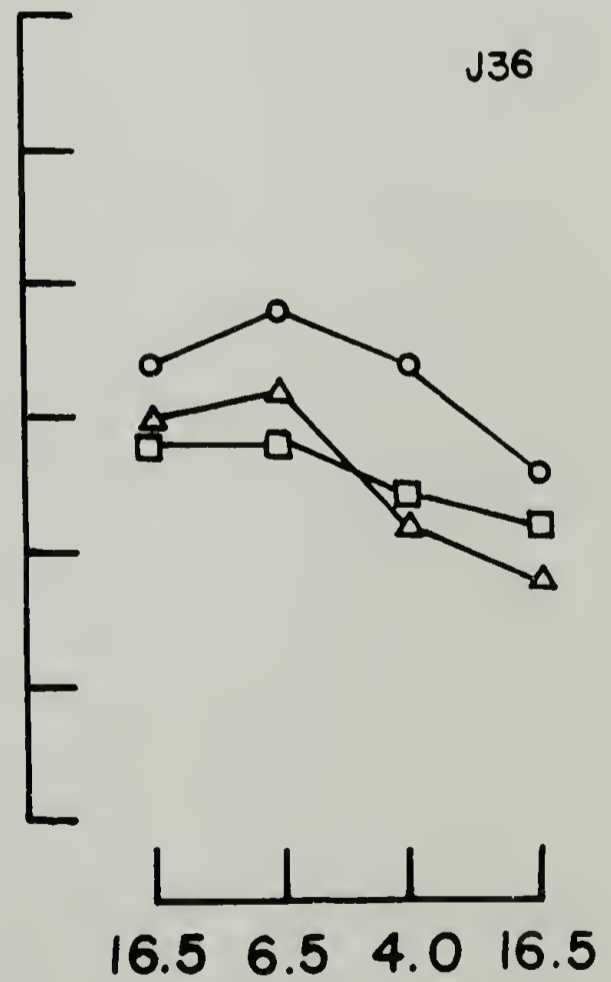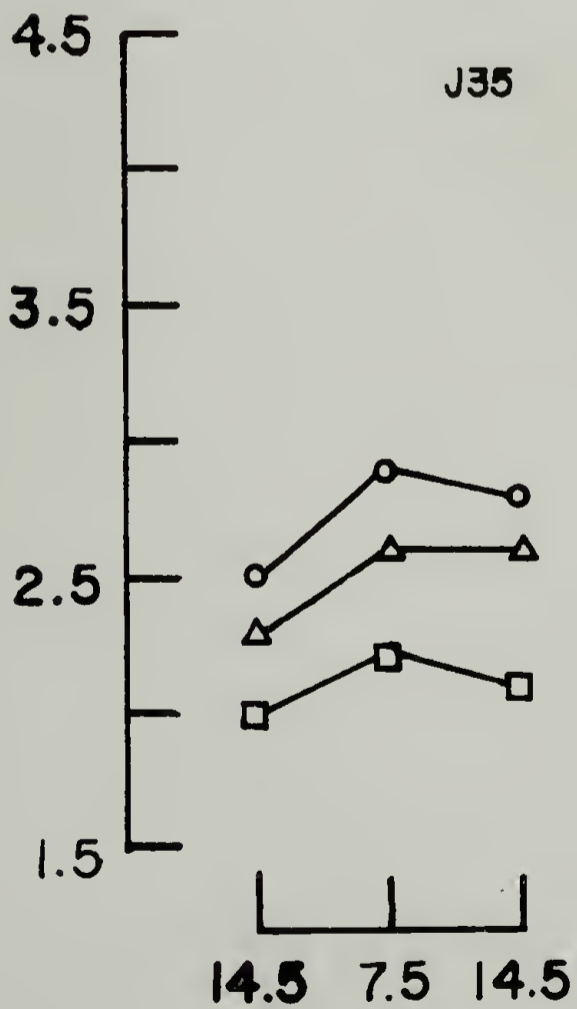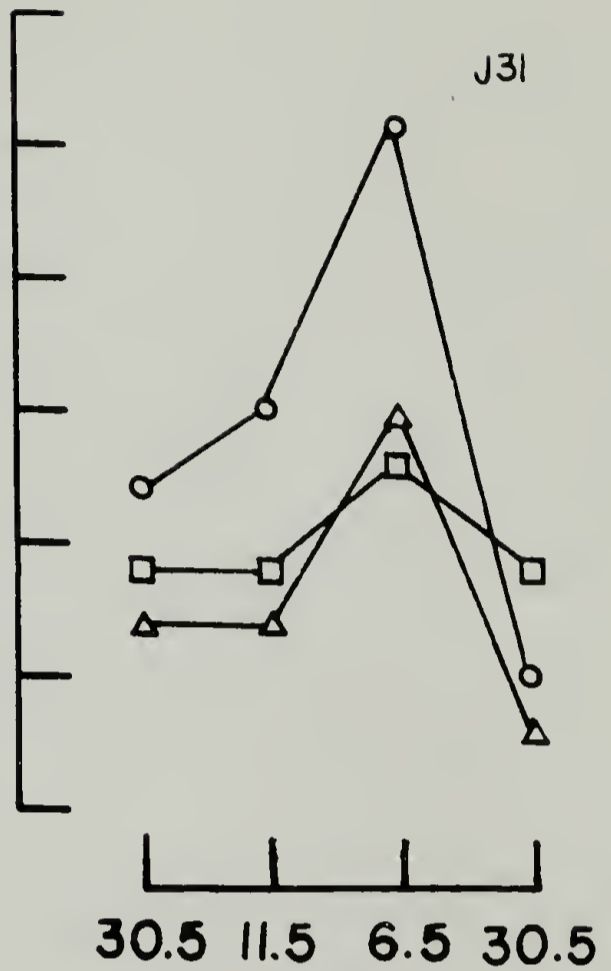
VIEWING TIME (SECS)

Figure 8. The rate of prey capture (number of prey taken per minute spent searching for each viewing time. The data for the individual jays are graphed for each set.
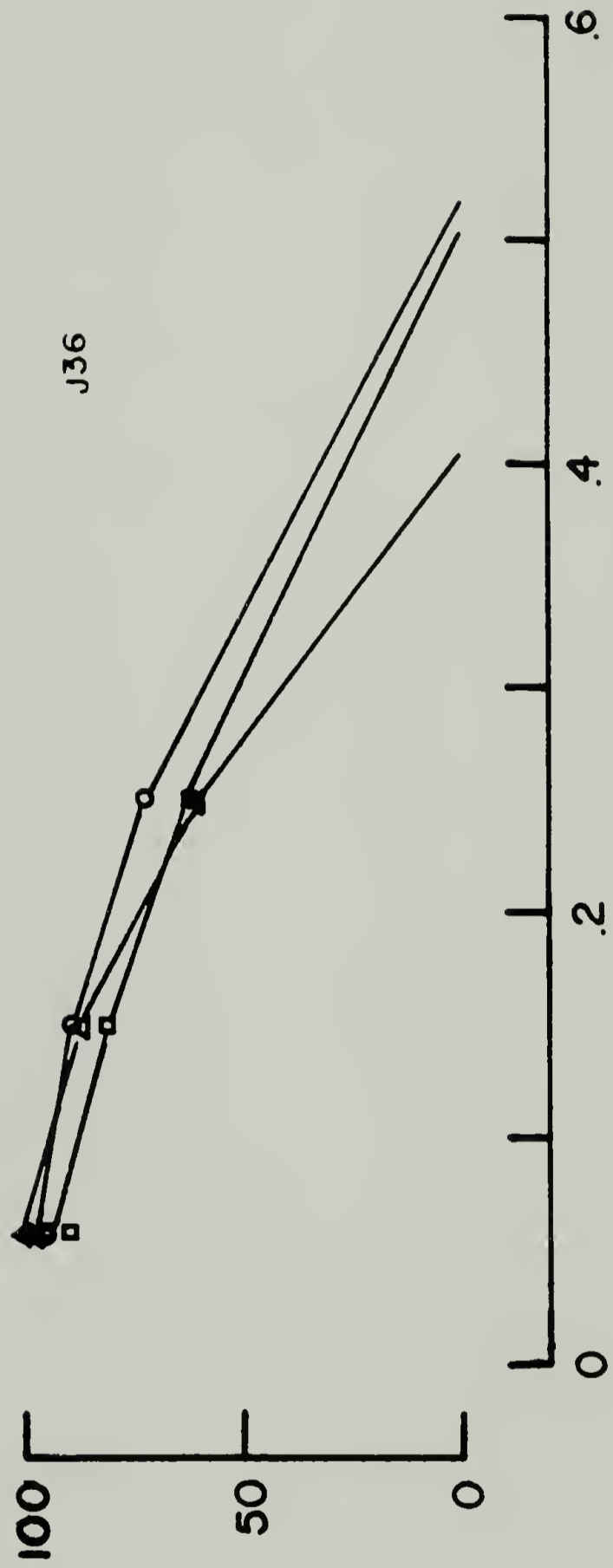
Figure 9. Graph of the Gendron & Staddon model for J31 & J36, showing the percentage correct foor moth (positive) slides as a function of 1/viewing time (display duration). The curves were fitted by eye.
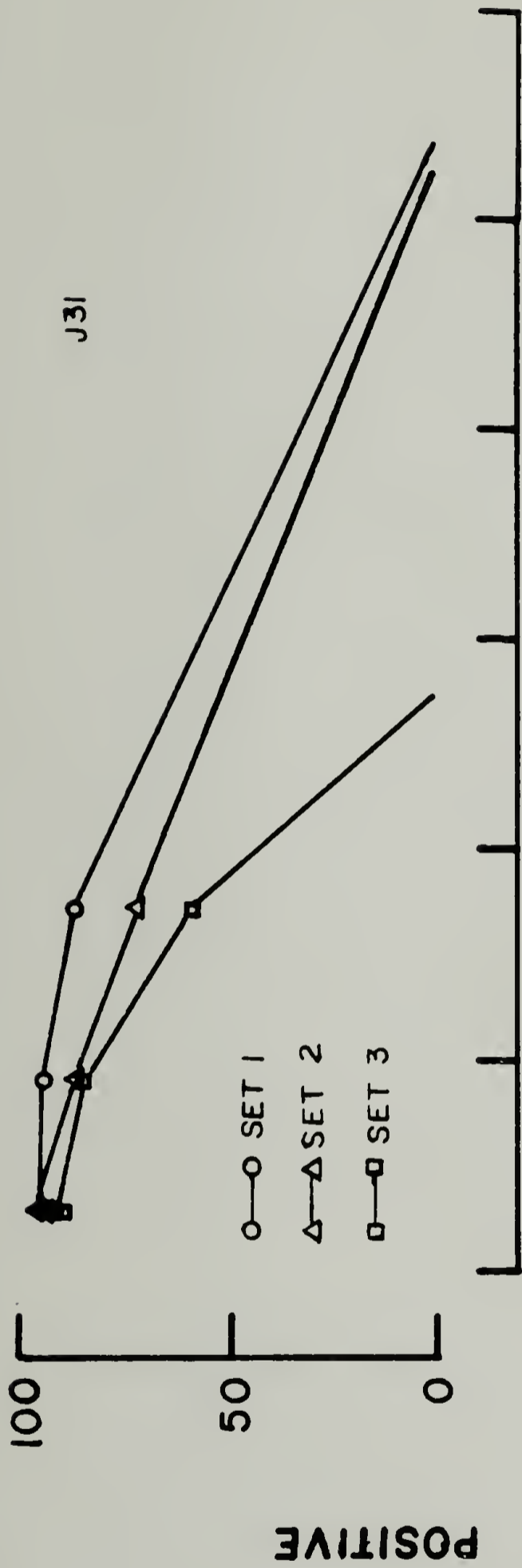
CHAPTER IV

DISCUSSION

General Discussion

Kamil, Endler & Olson (in prep) have shown that blue jays adjust their search time depending on the difficulty, or crypticity, of the slides. The results of the present experiment confirm this. Three slide sets were used to vary crypticity. Each set contained a white birch tree which varied in the proportion and patterning of black and white (see Figures 1-3). When C. relicta moths were placed on the trees, they ranged from visible (conspicuous) to difficult to detect (cryptic). Set 1, moth on white bark, was ranked easiest. This set had the shortest ATT, GUT and highest rate of prey capture. The moth slides for this set had the highest percentage correct and lowest percentage abort. As crypticity increased ATT & GUT lengthened and rate of prey capture decreased. The percentage correct decreased and percentage abort increased for the moth slides. Set 3 was ranked most cryptic and Set 2 was intermediate.

The problem with the Kamil, Endler & Olson (in prep) experiment was that they were unable to determine whether the jays were as efficient as possible for any crypticity level encountered. The present experiment attempted to answer this question. The time available for the jays to

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view the slides was varied. If the jays were performing efficiently, they should be spending the minimum time necessary per prey taken (maximizing rate of prey capture). Reductions in viewing time should not affect rate of prey capture. There should not be any differences between the predicted and obtained ATT, GUT and percentage abort. Two jays, J5 & J36, were shown to be efficient. These jays were maximizing their rate of prey capture by adjusting their search times based on crypticity.

Two jays, J31 & J35, did not show maximum efficiency. These jays showed an increase in rate of prey capture and decreases in ATT, GUT and percentage abort as viewing time decreased. The time available to make a decision, as well as crypticity, was used by these jays to adjust their search times. The only benefit which might result from this behavior is the occasional detection of more prey. There is some indication this might happen. For the longest viewing times, percentage correct for moth slides and rates of prey capture for each set were averaged as if there had been two groups, J5 & J36 in one group and J31 & J35 in the other group. J31 & J35 averaged 4.7% higher percentage correct (range -0.7 to 10%) at a rate of prey capture cost of 0.3 (range -0.6 to -0.1) below J5 & J36.

Two results obtained in this study were not expected. First, when viewing time was reduced there was an unexpected increase in aborts for no-moth slides. It is

unlikely this was due to the jays not having enough time to respond to the slides, since the reductions in viewing time were based on the previous performance of the jays. One explanation might be the difference in reinforcement for moth and no-moth slides. Only correct responses to moth slides were reinforced. Although all jays responded to the moth slides, regardless of viewing time, they responded to no-moth slides only at the longest viewing times. If the jays had been reinforced for correct responses for no-moth slides, they might have continued to respond to these slides when the viewing time was reduced.

The second unexpected result was the reversal in crypticity ranking for no-moth slides based on percentage correct and percentage abort. The results of the Kamil, Endler & Olson (in prep) experiment showed the same rankings for moth and no-moth slides. In the present experiment Set 3 was ranked most cryptic for all dependent variables except percentage correct for no-moth slides, where it was ranked easiest. Set 1 was ranked easiest for all dependent variables except percentage correct for no-moth slides, where it was ranked most cryptic. Set 2 had an intermediate ranking for all dependent variables.

This may have been due to the different procedures used in the two experiments. In the Kamil, Endler & Olson (in prep) experiment eight slide sets were randomly shown

each session. In the present experiment only one slide set was shown in a session. When all the slides are difficult, the jays may find searching the slides more aversive than when the slides are all easy.

This suggests the jays may also be using patch crypticity (the average crypticity of all the slides) to adjust their search times. If this is the case, when the patch has mixed crypticity the jays may decrease their search time for easy slides, since the next one will be more difficult, and increase their search times for cryptic slides. This might result in the same crypticity rankings for percentage correct for moth and no-moth slides. This prediction for the mixed patch situation seems counterintuitive. However, based on the data of the present experiment, if the jays were adjusting their search times based on the crypticity of the present site and the probability of the next site being more or less cryptic, these predictions may hold.

Future Research

Three experiments are suggested by this experiment. Two experiments would examine the effects of reinforcement and patch crypticity for moth and no-moth slides. The third experiment would focus on the application of the Gendron & Staddon (1983) model for the present cryptic prey simulation.

Experiment 1

The first experiment would focus on the jays differences between moth and no-moth slides. First, the jays show longer giving-up times than attack times. Second, when viewing time was decreased, there was an unexpected increase in aborts for no-moth slides, but not for moth slides.

There are two possible explanations for the GUT and ATT differences. First, moth slides contain a distinctive feature, moth on bark, whereas, the no-moth slides do not contain such a feature. This should make moth slides more salient than no-moth slides, forcing the jays to search the no-moth slides longer. Second, if the jays are attempting to maximize prey capture and no moth has been detected, it may be to the jays' benefit to search longer, since occasionally a moth will be detected. The jays could have correctly identified the slide as a no-moth slide sooner, but the longer search time allowed them to increase the number of moth slides correctly identified.

The only explanation which seems likely for the increase in aborts for no-moth slides is the difference in reinforcement. Only correct responses for moth slides were reinforced. Although the jays responded to no-moth slides at long viewing times, they quit responding to these slides when the viewing time was reduced. This did not happen for the moth slides. This indicates that if the jays had been

reinforced for correctly responding to the no-moth slides, they would not have quit responding when the viewing time was decreased. This was not done in the present experiment since it would have defeated the purpose of accurately simulating a cryptic prey detection task.

One possible procedure which might be used to look at the differences between the moth and no-moth slides would be to vary reinforcement and viewing time. If the jays were reinforced for correctly responding to moth and no-moth slides as viewing time was varied, the effect of reinforcement on the ATT, GUT and aborts could be predicted.

The effect of reinforcement on the jays' aborts is relatively easy to predict. If the failure of the jays to respond to no-moth slides when viewing time was reduced was due to nonreinforcement, the jays should continue to respond to no-moth slides when correct responses are reinforced and viewing time is reduced.

The effect of reinforcement on ATT & GUT is more interesting. If the differences in these latency measures were due to presence vs. absence of a feature, when correct responses to no-moth slides are reinforced the differences in ATT & GUT should remain. However, if these differences are not feature related, and the jays are searching longer because it occassionally pays off, then

GUT should decrease when correct responses for no-moth slides are reinforced.

Experiment 2

The second experiment indicated by the present results would focus on what effect patch crypticity might have on search time when no moth has been detected. If the area that is currently being searched is considered a site, the patch would consist of all available sites. The patch crypticity could be the same for all sites or consist of mixed sites. The results of the present experiment indicate that patch crypticity might affect the search time of the jays when no-moth has been detected. The jays were more likely to search longer when patch crypticity was easy than when it was cryptic. This caused more aborts more for no-moth slides when the patch was easy than hard. It is possible that this was due to the limits imposed on the viewing time, but this seems unlikely since the longest viewing time was chosen so no or few aborts would occur.

Assuming it was patch crypticity which affected search time when no moth had been detected and the jays were attempting to maximize the number of prey captured, predictions, based on data from the present experiment, can be made about what should happen when the patch has mixed crypticity. Since the crypticity of the next site to be encountered cannot be predicted, there should be a decrease in the long search times, resulting in decreased aborts,

for easy sites. There should be a corresponding increase in aborts for difficult sites, since the next site will most likely be easier; allowing the jays to spend more time searching the slide if no moth has been detected. If patch crypticity does not affect the search time when no moth has been detected, there should be no difference between single and mixed patch crypticity.

Experiment 3

The third experiment would be a more rigorous test of the Gendron & Staddon (1983) model. The main problem with the present procedure was too few viewing times were used and exact crypticity level, optimal and maximum search rates could not be determined. The results of the analysis for two jays (J31 & J36), however, indicated the slide sets used were not very cryptic for the jays.

There are three possible explanations for the low level of crypticity. First, the model does not apply to the present situation. The seems unlikely since the procedure used appears to meet all the requirements of the model and is quite similar to the procedure used by Gendron & Staddon (1984) for human subjects.

The second explanation for the low degree of crypticity would be the prior experience of the jays with the slide sets. This could have caused a change in the crypticity index. However, the Gendron & Staddon (1983)

model assumes that if a search image is formed, it has reached its asymptotic level. Therefore, the previous experience with the slides would fulfill the search image requirement and cannot explain the low degree of crypticity.

The third reason for the low degree of crypticity may have been the cost for making an error. Only 25% of the slides presented each session contained a moth. Therefore, the maximum reinforcement for a session was low. Missing a moth slide resulted in decreased reinforcement and decreased foraging efficiency. Incorrectly responding to a no-moth slide, as if it had been a moth slide, forced the jays to sit through the 30 sec. handling time with no reinforcement at the end of the handling time.

This implies that error costs and/or density may have an effect on the level of crypticity. The model predicts that density should have no effect on the level of crypticity. It does not make any predictions about error costs. However, even if the cost of making errors was affected by the crypticity level, when density is held constant the effect might be the same for all levels of crypticity. Thus, density and cost of making errors do not seem to be able to explain the low level of crypticity for the slide sets.

The Gendron & Staddon (1983) model seems to be correct and the slide sets used, overall, were not very cryptic to the jays. To accurately test the Gendron & Staddon (1983) model different slide sets, possibly C. retecta on oak, shown at more viewing times should be used. Then exact crypticity levels, optimal and maximum search rates could be empirically determined. Density could be manipulated to test whether it will have an effect on crypticity level.

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    Journal of Lepidopterist's Society, 27:175-192.

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