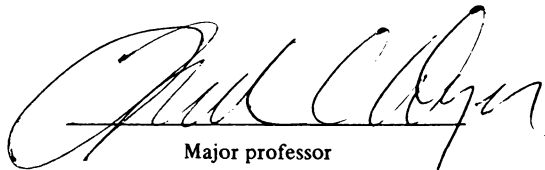This is to certify that the

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FORAGING BY CHICKS FOR TWO TYPES
OF CRYPTIC PREY: A TEST OF THE
SEARCH IMAGE HYPOTHESIS

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Karen Ruth Cebra

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FORAGING BY CHICKS FOR TWO TYPES OF CRYPTIC PREY: A TEST OF THE SEARCH IMAGE HYPOTHESIS

By

Karen Ruth Cebra

A THESIS

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the Degree of

MASTER OF SCIENCE

Department of Zoology

1990

ABSTRACT

FORAGING BY CHICKS FOR TWO TYPES OF CRYPTIC PREY: A TEST OF THE SEARCH IMAGE HYPOTHESIS

By

Karen Ruth Cebra

Support for the existence of perceptual specializations, or search images, for a given prey type has recently been challenged using the search rate hypothesis. In this series of experiments domestic chicks (*Gallus gallus*) were used to test for the property of interference that is predicted by the search image hypothesis but not by the search rate hypothesis. Initial experiments determined two prey types (colored rice grains) which were equally preferred, distinguishable, and of equal crypticity. Experiments designed to test for interference presented the two prey types simultaneously on a cryptic background. No evidence for interference was found over the course of entire or successive trials, but some evidence, in the form of runs on a single prey type, exists for interference within a trial.

To Daniel, without whom this work would never have been done.

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Chapter I

INTRODUCTION

The behavior of a forager affects not only the individual, but also the population dynamics of the prey species. If the predator nonrandomly selects prey, the effect of the predation will be a selective pressure upon the prey population (Clarke 1979). For example, it has been demonstrated that preferential selection of the most common phenotype can result in apostatic selection (switching) which will contribute to the maintenance of genetic diversity (Clarke 1962, Allen 1974, Murdoch and Oaten 1975, Cornell 1976, Cooper 1984). One postulated behavioral mechanism that could produce this effect involves the formation of a 'search image' (see review in Krebs 1973) - a term which has often been applied more broadly than originally intended (Lawrence and Allen 1983). Here it is used, as originally intended by Tinbergen (1960) and Dawkins (1971a), to refer to a 'change in the ability of a predator to detect cryptic familiar prey' (Lawrence and Allen 1983). More specifically, 'search image' refers to 'perceptual changes in the predator that temporarily increase its ability to detect particular cryptic prey as a result of recent encounters with similar cryptic prey' (Guilford and Dawkins 1987). A key property of a search image for a given prey type is that it interferes with the predator's ability to detect other prey types (Croze 1970) which may result in a preference (Krebs 1973). It is this property that isolates the 'search image' mechanism from other types of learning that could

1

account for a preference for a given prey type as postulated by Krebs (1973). As summarized by Lawrence and Allen (1983) these include learning to:

- find food in a specific place,

- search in an appropriate habitat type,

- adjust the search path to maximize prey encounter probability,

- prefer or avoid a given prey type over others independent of the predator's ability to see the different types (i.e. prey of varying palatability or familiarity),

- utilize specific hunting techniques, for example, search rate modification, and

- improve the ability to handle prey.

Though all of these types of learning may lead to a preference for a prey type, none of them will change the predator's ability to *detect* one prey type over another as a search image would.

Many experiments enlisted in support of the search image hypothesis have recorded improvements in the ability of predators to detect and capture cryptic prey (de Ruiter 1952, Kettlewell 1955, Clarke 1962, Dawkins 1971a, Pietrewicz and Kamil 1979, Lawrence 1985a, b, 1986, Gendron 1986). Recently, Guilford and Dawkins (1987) have challenged several studies (Dawkins 1971a, Pietrewicz and Kamil 1979, Lawrence 1985a, b, 1986, Gendron 1986) employing this type of evidence in support of perceptual specialization as a foraging tactic because it fails to exclude other hypotheses which could also account for improvements in the capture rate as a function of recent experience, but without perceptual specializations. The same criticisms put forth by Guilford and Dawkins (1987) can be applied to Croze's (1970) work

on Carrion Crows, which Krebs (1973) cites as the 'only detailed attempt so far to investigate the mechanism of searching-image formation in the field.'

As an alternative to search images, Guilford and Dawkins (1987) offer the 'search rate hypothesis', a 'slightly reinterpreted version' of Gendron and Staddon's (1983) optimal search rate hypothesis. In this scenario, a predator is faced with a trade-off between foraging speed and detection accuracy - an increase in search speed decreases the probability of detecting the prey but increases the encounter rate whereas a decrease in speed increases the probability of detection but decreases the encounter rate (Gendron and Staddon 1983, Guilford and Dawkins 1987). The optimal search speed is one in which prey capture is maximized. Clearly, an increased ability to detect one cryptic or conspicuous prey type should not interfere with the detection of other equally cryptic or conspicuous prey as it would if search images were employed. Nevertheless, the search image and search rate hypotheses result in similar foraging behavior in other ways. Both predict that detection accuracy increases for cryptic prey as a result of recent encounters with that prey type, and both predict that frequent encounters with conspicuous prey interfere with the ability to detect cryptic prey. In addition, both predict that an increased ability to detect conspicuous prey decreases the ability to detect cryptic prey (Guilford and Dawkins 1987).

The purpose of the present work was to test for the interference predicted by the search image hypothesis using experiments modeled closely on those in the original study by Dawkins (1971a); 'predators' (domestic chicks) were given 'prey' (artificially colored grains of rice) on backgrounds colored to make the prey appear cryptic or conspicuous. Domestic chicks were chosen because of the ease with which the experimental conditions could be controlled. Also, as Dawkins points out, rice grains were chosen to keep the experiments 'as *natural* as possible, by observing the chicks performing a common part of their behavioral repertoire, i.e. pecking food from the

ground' (Dawkins 1971a). The key difference between the present work and all previous experimental studies is that predators were given a simultaneous choice of two different but equally preferred and equally cryptic prey colors (=types). If a changed ability to take one prey type automatically interferes with the ability to take the other type, then the two types should be taken at different rates, as a strict interpretation of the search image hypothesis would predict. The search rate hypothesis does not predict interference. A direct test of the search rate hypothesis is not possible in this study because the individual parameters that make up search rate (for example handling time and area searched) are not measured, and because the experiment does not prevent birds from modifying their search rates. Nevertheless this study isolates the question of whether a change in the ability to take one prey type interferes with the ability to take another type.

Chapter II

METHODS

A   General Methods

As in Dawkins' (1971a) study, domestic chicks (*Gallus gallus*) were used as 'predators' and colored rice grains were used as 'prey'. Freshly laid White Leghorn eggs were obtained from a commercial hatchery and incubated. Upon hatching, chicks were moved to a brooding pen (Figure II.1) and maintained on a light:dark cycle standardly used for commercial production - 24:0 for days 1-3, 23:1 for days 4-6 and then 14:10 from day 7 on. At seven days of age, they were moved to group cages (Figure II.2) and raised to the testing age of 28 days, when they could be sexed reliably (Figure II.3). During this period chicks were fed commercial chick starter feed and supplied with water *ad libitum*. Food and water were replenished at regular intervals in order to establish consistency throughout the experiments.

The behavior of the chicks was observed in an arena measuring 60 X 60 X 45 cm high (after Dawkins 1971a) and was made of white tempered hardboard (Masonite Corp.). The floor was either a 60 X 60 cm piece of white tempered hardboard (preference and discrimination experiments) or a 60 X 60 cm piece of white tempered hardboard with two colors of aquarium gravel (Spectrastone by Wil-Marox) glued to it with clear-drying epoxy (experiments with cryptic prey). Figure II.4 shows a view
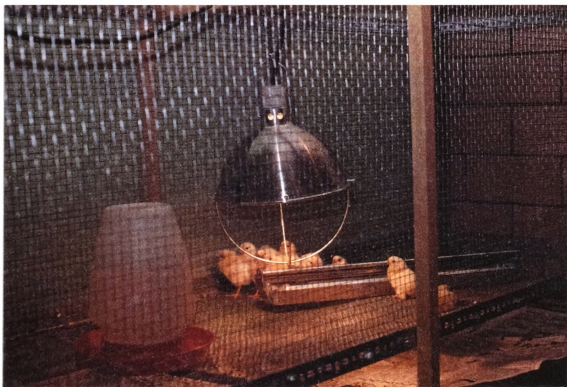
Figure II.1: A photograph of the brooding pen. A heat lamp is provided.

Figure II.2: A photograph of the group cages. Each tier could house up to 12 chicks.

Figure II.3: Photographs of (a) a female chick and (b) a male chick at 28 days of age. Note the more pronounced red comb and wattle of the male.

of the testing arena being prepared for the experiments with cryptic prey. The gravel was mixed in equal proportions prior to gluing and then scattered over the wet glue and allowed to dry thoroughly. Careful attention was paid to ensure equal intensity of the two colors of gravel with respect to each other. Rice grains were dyed with food coloring (Dec-a-Cake by Durkee Famous Food Inc.) to match as closely as possible by human eye the colors of the aquarium gravel using the following recipe.

Ingredients :

1. 170 ml rice

2. 170 ml water

3. Drops of food coloring for:

   - Orange: 12 drops yellow, 8 drops red

   - Red: 30 drops

   - Green: 20 drops

   - Yellow: 10 drops

Procedure: Mix rice, water, and food coloring thoroughly; allow to soak 6 hours and then spread on newspaper to dry; stir occasionally to prevent rice from sticking.

Green and orange were chosen based on Dawkins' (1971a) study. Red and yellow were chosen as possible colors because they could be prepared easily without mixing colors. Blue and violet hues were avoided because a chicken's vision is not sensitive to light of those frequencies (Bowmaker and Knowles 1977). Figure II.5 shows the various colors used or considered for these experiments.

Approximately 700 grains (11 grams) of each of the two colors to be used in the experiment were mixed together and then scattered on the floor of the arena. Chicken

Figure II.4: A photograph of the testing arena used for the experiments with cryptic prey.

Figure II.5: A photograph of the various colors of rice grains.

wire covered the arena to prevent chicks from escaping. The observer watched the chicks from above as shown in Figure II.6.

Over a 7 day period starting at 21 days of age, chicks were acclimated in groups to the test arena, to the presence and voice of an observer, and to colored rice grains as food. Acclimations began about 1 hour after the lights came on and ended when all the chicks had been exposed to test conditions once. At the start of each day of acclimation or experimental testing, chicks were marked for individual identification with India ink as shown in Figure II.7. The food trays were removed from the group cages just before the lights came on so that the chicks would be hungry for the acclimation runs. A group of 3 to 5 chicks were placed in the test arena with colored rice for 15 minutes while an observer made oral comments about their behavior. Over the 7 days of acclimation, an effort was made to group chicks such that individuals foraged with as many of the other individuals as possible.

After the seven days of acclimation, the chicks were divided according to sex and then assigned randomly to be either focal chicks (whose behavior was recorded) or companion chicks (whose behavior was not recorded). Since chicks become agitated when alone (Dawkins 1971a) a companion chick had to be placed in the arena with each focal chick. Neither companion nor focal chicks were used in more than one experiment, but within an experiment, chicks could be used in multiple trials. Companion chicks could be paired with more than one focal chick in any given experiment. In no pair were two males placed together since two males tend to fight with one another rather than forage. Figure II.8 shows a focal-companion chick pair foraging on a white background.

Each experimental trial began with the introduction of a focal chick and a companion chick into the arena (the companion chick was always put in first so that the focal chick was never alone in the arena) and ended after the focal chick had eaten a

Figure II.6: Observations of a trial. The observer records the number of grains taken of each color both orally and with handheld counters shown above.

Figure II.7: A photograph of a marked chick. Chicks' toes were numbered 1 through 6 starting from the left. No chick had more than two toes marked. This chick is marked number 1.

Figure II.8: A photograph of a pair of chicks foraging. The companion chick is in the back.

specified number of grains or had foraged for a specified maximum amount of time, whichever came first (refer to sections B, C, and D in chapter II for specific details). The observers oral comments about the colors of 'prey' selected by the focal chick were tape recorded and later transferred to computer for analysis. The computer program 'TIMER' (see Appendix A) was used for the transfer. It recorded the color and time for each of the strikes over the course of a trial into a data file. A plot of cumulative rice grains of each color against time could be made from these files so that the net rates at which each color was selected could be calculated.

B   Preference Experiments - Methods

The goal of the preference experiments was to find a pair of artificial prey colors which the chicks preferred equally well, thus minimizing the confounding influence of color preference in subsequent experiments. Four pairs of colors were tested: green and red, yellow and orange, orange and red, and yellow and red. Ten focal chicks were tested on each combination. About 700 grains of each color were scattered on a white floor in the arena. The focal chick was observed until it had eaten a total of 75 grains or had foraged for 15 minutes, whichever came first. Each focal chick was tested only once (a total of 40 chicks - green-red: 4 males, 6 females; yellow-orange: 4 males, 6 females; yellow-red: 3 males, 7 females; orange-red: 5 males, 5 females); the same set of seven companion chicks was used for each of the four color combinations.

Two colors were determined to be equally preferred if the chicks chose them at equal net rates (as determined in the analysis of the cumulative number of grains of a particular color chosen versus time) over a trial.

C   Discrimination Experiments - Methods

To determine whether chicks could distinguish between the two colors found to be equally preferred (red and orange), rice grains of one of the two colors were made distasteful. In the first experiment, orange was made distasteful by soaking the rice for 6 hours in a solution of 4 g quinine sulfate and 2 g of powdered mustard per 100 ml of dye solution (Gittleman and Harvey 1980). In the second experiment red was made distasteful. If chicks are able to discriminate between red and orange, then they should be able to learn to avoid the distasteful color. About 700 grains of each color were scattered on a white background and the focal chick was observed until it had eaten 75 grains or until 7 minutes had elapsed, whichever came first. During the preference experiments, it was determined that any pattern would be obvious by 7 minutes. For each of the two experiments, 10 focal chicks (5 males and 5 females) and 6 companion chicks were presented with one of the colors distasteful. Trials were repeated four times at hourly intervals, so that each chick was observed for a total of five trials.

D   Experiments with Cryptic Prey - Methods

In order to test whether an ability to take one prey type interferes with the ability to take another equally cryptic prey type, a total of 11 male and 11 female focal chicks were given the opportunity to forage for red and orange rice grains, which had been determined to be equally preferred and distinguishable by the chicks in the prior experiment, on a background of red and orange aquarium gravel. The gravel was glued to the floor such that chicks were unable to dislodge it either by pecking or scratching. In addition, chicks were able to learn quickly the difference between gravel and 'prey' and thus did not waste time pecking at gravel.

Two experiments were performed. In the first, performed with 10 focal chicks (5 male and 5 female) and 2 companion chicks, a focal chick and companion chick pair was placed into the arena with about 700 grains each of red and orange rice grains and observed until the focal chick had eaten a total of 75 grains or had foraged for 7 minutes, whichever came first. Trials were repeated two times at hourly intervals, so that each chick was observed for a total of three trials.

The second experiment, with 12 focal chicks (6 male and 6 female) and 4 companion chicks was similar to the first except that each chick was exposed prior to the trial to an introductory arena where approximately 60 grains of one of the two colors was spread on a white background. 3 males and 3 females, with companions, were introduced to red, and 3 males and 3 females were introduced to orange. Chicks were transferred from the introductory arena to the arena with cryptic prey after the focal chick had eaten 10 grains (Dawkins 1971b) or had foraged for 30 seconds, whichever came first. The goal was to determine whether prior experience with a single prey type would affect later choice behavior when chicks were subsequently presented with two prey types.

Chapter III

RESULTS

A Preference and Discrimination Experiments

Two simultaneously presented colors were considered to be equally preferred if the following two conditions were met. First, there should not be a significant difference between the rates, as measured by the cumulative number of grains taken over time averaged for a sample of chicks, at which each color was taken. Figures III.1 through III.4 show the behavior of individual chicks for the preference experiments plotted as the cumulative number of grains selected against elapsed time. The average rate at which each color was selected is shown in Table III.1. For chicks tested on two of the combinations, green-red and yellow-orange, clear preferences were observed (t-test, 0.05 level; and refer to Figures III.1 and III.2, and Table III.1). For chicks tested on orange-red and on yellow-red, the t-test showed no statistically significant preference (refer to Figures III.3 and III.4, and Table III.1).

Second, there should be no significant tendency for individual chicks to specialize on one color or the other irrespective of whether the intake rates averaged across chicks were the same. This condition would be violated if some chicks were to take one color predominantly and others were to take the other color, resulting in equal average intake rates. This tendency was measured by calculating an 'asymmetry
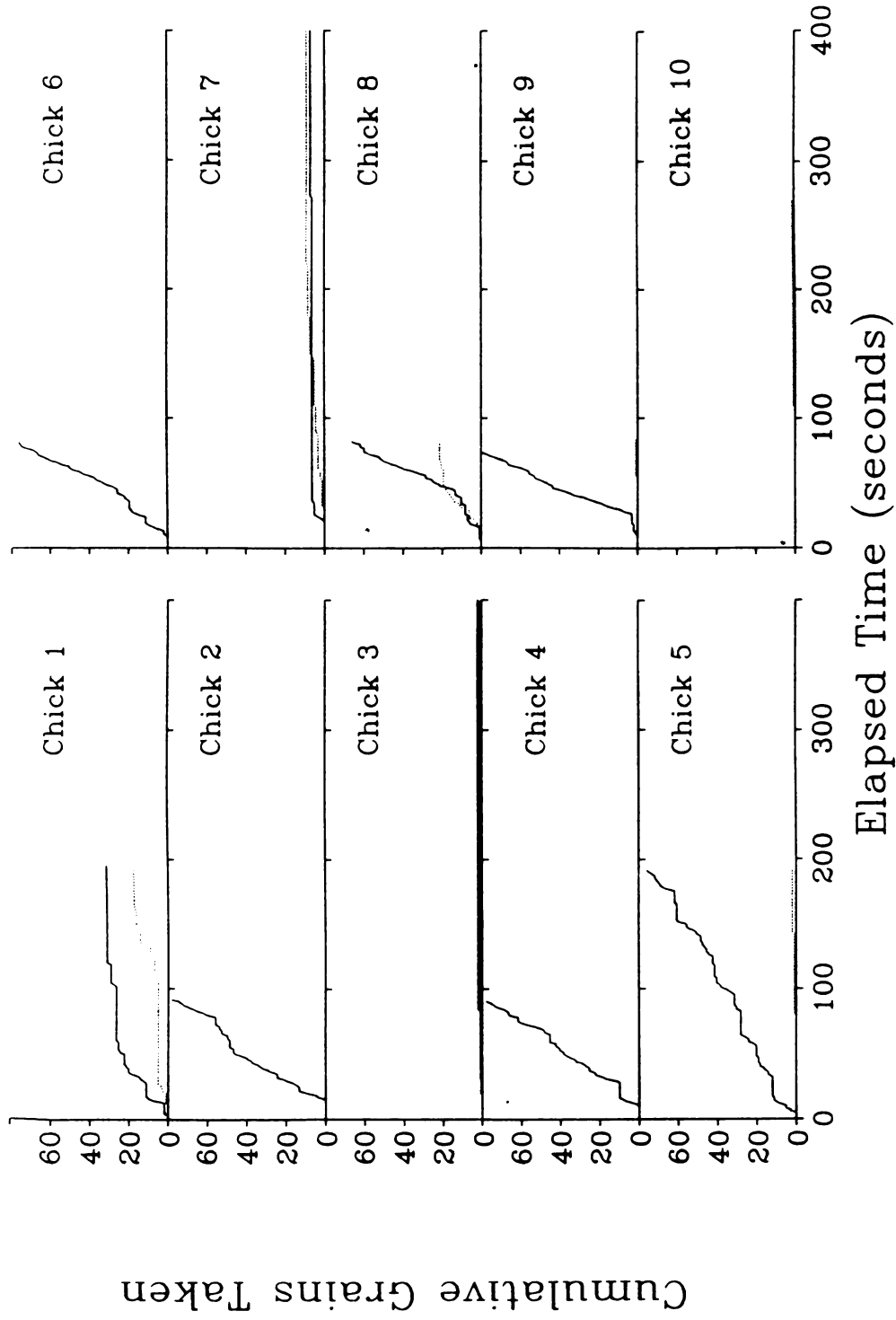
Figure III.1: A plot of the cumulative grains taken as a function of time for each of the 10 focal chicks in the green-red preference experiment. The dotted line corresponds to green grains while the solid line corresponds to red grains.
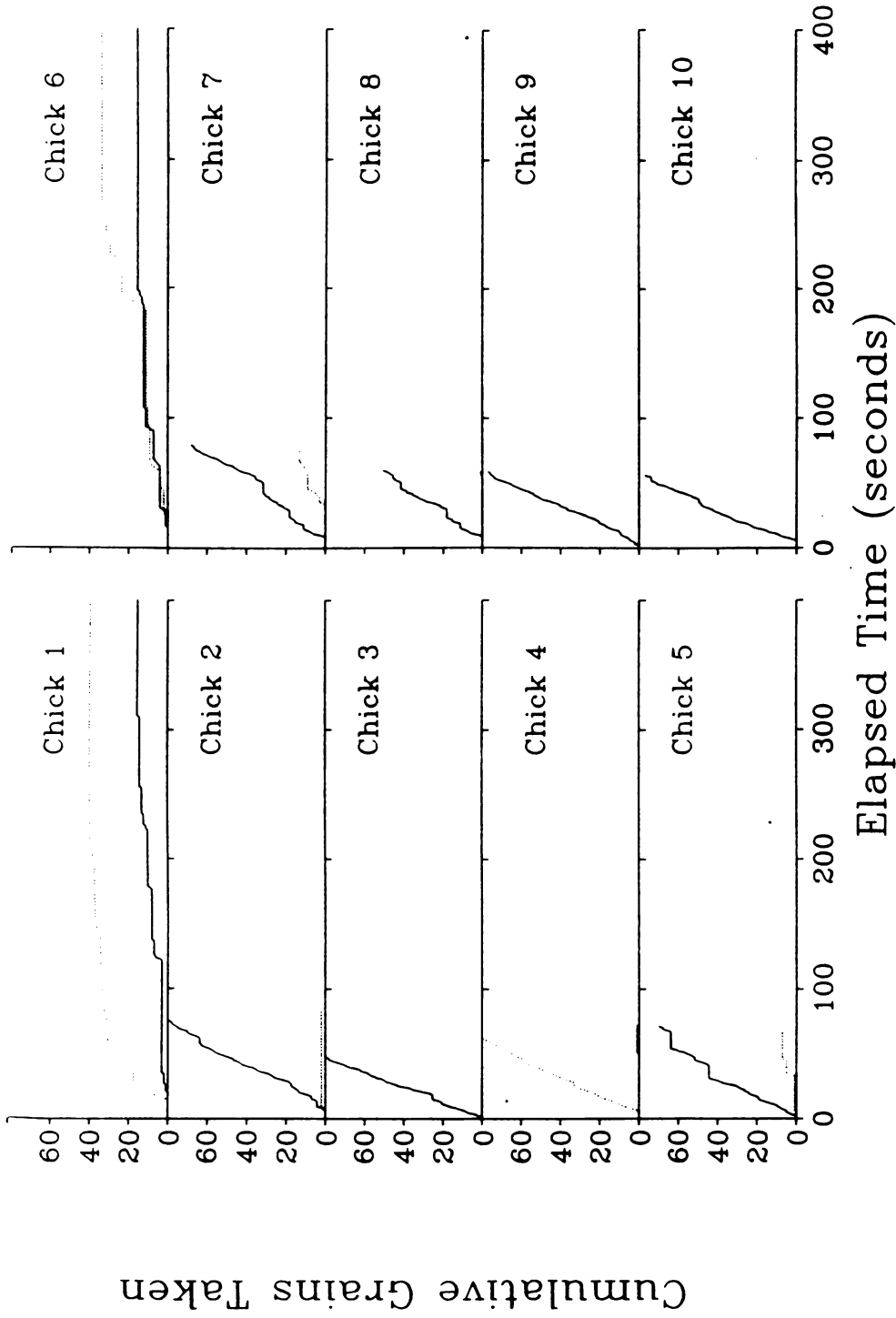
Figure III.2: A plot of the cumulative grains taken as a function of time for each of the 10 focal chicks in the yellow-orange preference experiment. The dotted line corresponds to yellow grains while the solid line corresponds to orange grains.
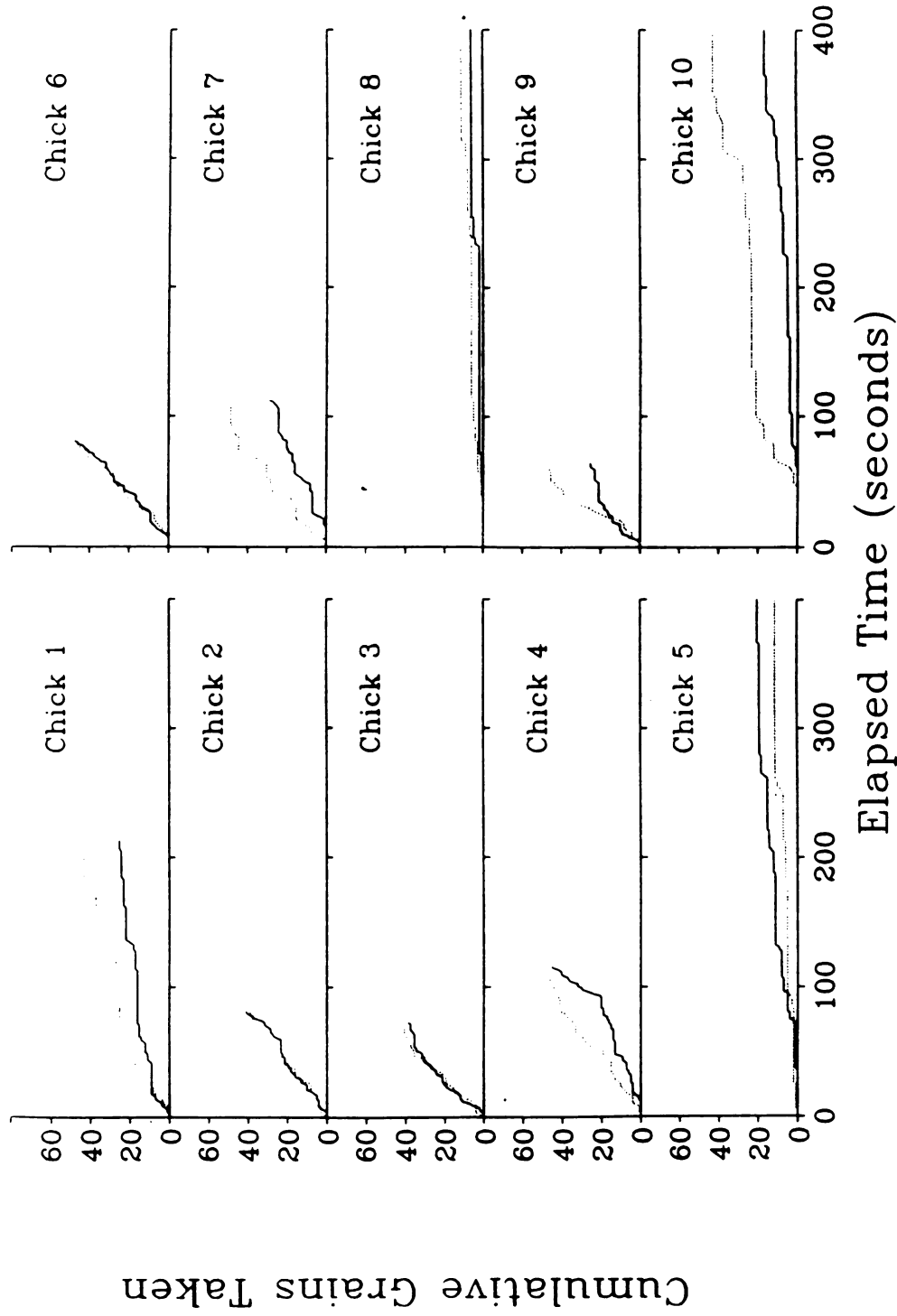
Figure III.3: A plot of the cumulative grains taken as a function of time for each of the 10 focal chicks in the orange-red preference experiment. The dotted line corresponds to orange grains while the solid line corresponds to red grains.
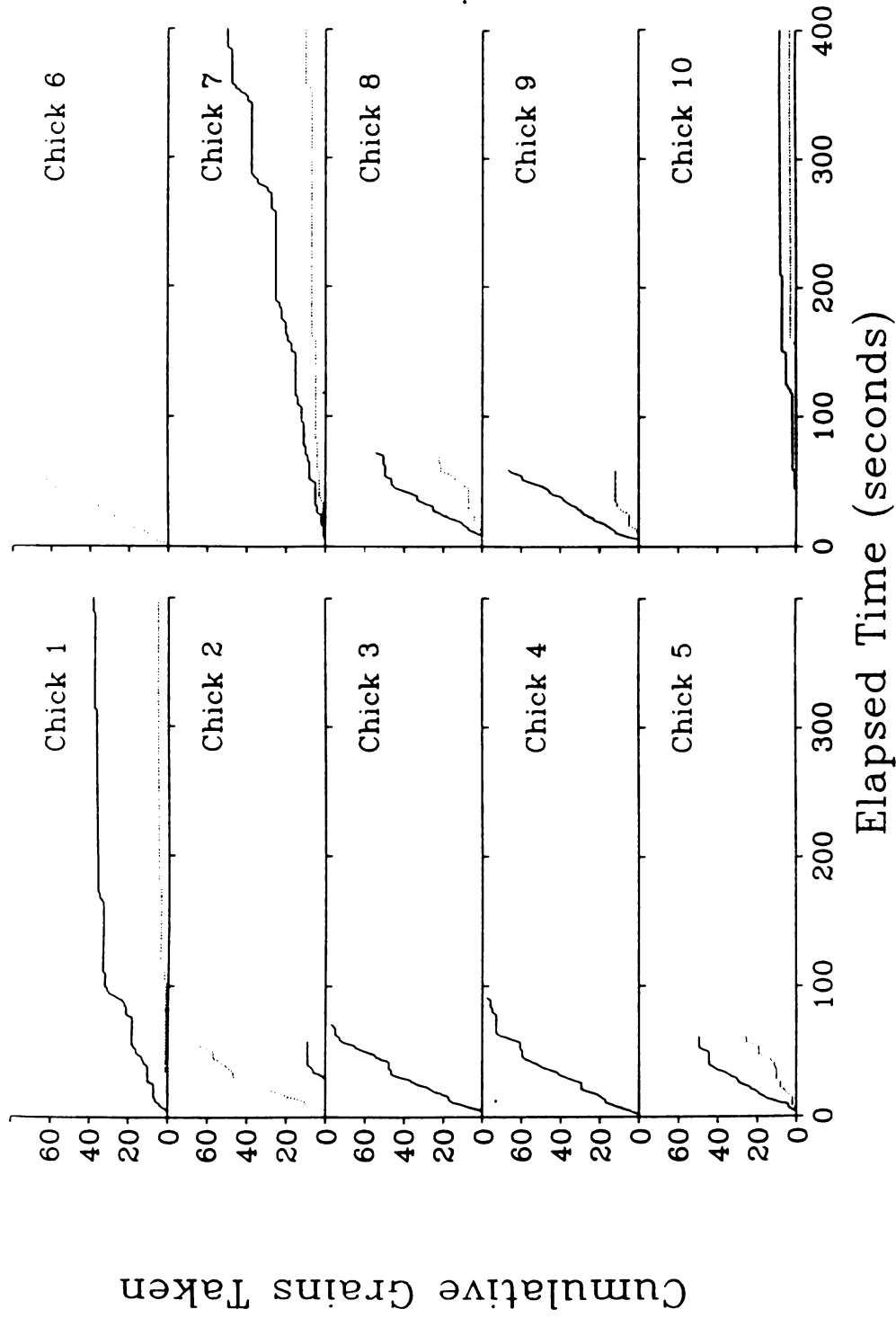
Figure III.4: A plot of the cumulative grains taken as a function of time for each of the 10 focal chicks in the yellow-red preference experiment. The dotted line corresponds to yellow grains while the solid line corresponds to red grains.

Table III.1: The average rate of intake for the various color combinations in the preference study experiments. The * indicates a significant t-test, 0.05 level.

Color Pair	Mean Grains/Sec	Significance
Green vs. Red	.04 ± .07 .51 ± .37	*
Yellow vs. Orange	.18 ± .38 .81 ± .59	*
Orange vs. Red	.36 ± .27 .28 ± .22	N.S.
Yellow vs. Red	.33 ± .46 .49 ± .46	N.S.

value' $(A.V.)$ for each chick as follows:

$$A.V. = \begin{cases} (rate_A - rate_B/(rate_A) & \text{if } rate_A > rate_B \\ (rate_A - rate_B/(rate_B) & \text{if } rate_A < rate_B \end{cases}$$

The asymmetry value ranges between 0 (no preference, total symmetry), and 1 (specific preference, total asymmetry). Table III.2 lists the asymmetry values for the yellow-red and orange-red combinations. If individual chicks choose randomly be-

Table III.2: Asymmetry values for Yellow-Red and Orange-Red color combinations. The * indicates a significant Mann-Whitney U test, 0.05 level.

Pair	Yellow-Red	Orange-Red
1	0.88	.47
2	0.87	.05
3	1.00	.07
4	1.00	.06
5	0.47	.26
6	1.00	.02
7	0.79	.40
8	0.59	.23
9	0.82	.51
10	0.56	.59
Significance	*	N.S.

tween colors, then large degrees of asymmetry are expected to be rare. Because asymmetry values can not take on negative values, a Poisson distribution corresponds to random selection of colors. The standard deviation represents the dispersion of individual responses. In order to generate an expected distribution to compare with the experimental distribution of asymmetry values, a computer simulation was run (refer to Appendix B). The simulation produced a Poisson distribution with standard deviation 0.2. The magnitude of the standard deviation was based on the deviations calculated from the experimental distributions. The experimental distributions were compared to the expected distributions using a Mann-Whitney U test. For yellow-red

the comparison yields significance and for orange-red no significance (Mann-Whitney U test, 0.05 level). This comparison shows that individual chicks demonstrate specific preferences for either yellow or for red when they are presented together. However, there is no such asymmetry for the orange-red combination. In addition, a t-test (0.05 level) showed no significant difference between the behavior of males and females in the orange-red study.

Of the pairs of colors tested, yellow-red met the first condition but not the second (Tables III.1 and III.2). Only orange-red met both conditions (Tables III.1 and III.2). Therefore, orange and red were chosen for use in the subsequent experiments.

Discrimination experiments showed that birds could distinguish orange and red grains. Figure III.5 illustrates the behavior of typical focal chicks over five successive trials in each of the two reciprocal discrimination experiments. Each chick's first trial confronted it with learning that one of the colors which had been previously palatable during the acclimation was suddenly distasteful. During the middle trials, the chicks showed a reluctance to eat anything, but began to choose proportionately more of the tasty color. By the final trials, the chicks had learned which of the two colors was tasty and chose that color almost exclusively. A Friedman's test (because of an overwhelming block effect, ANOVA's were not used) calculated for the reciprocal discrimination experiments (Table III.3) demonstrated that trial number had a significant effect on the relative rate at which grains were taken (0.05 level). The

Table III.3: Results of the Friedman's test showing the effect of trial number on the relative rate at which grains were taken. A * indicates a significant difference.

	Orange Distasteful	Red Distasteful
Calculated	20.72 *	11.2 *
Table	9.48	9.48
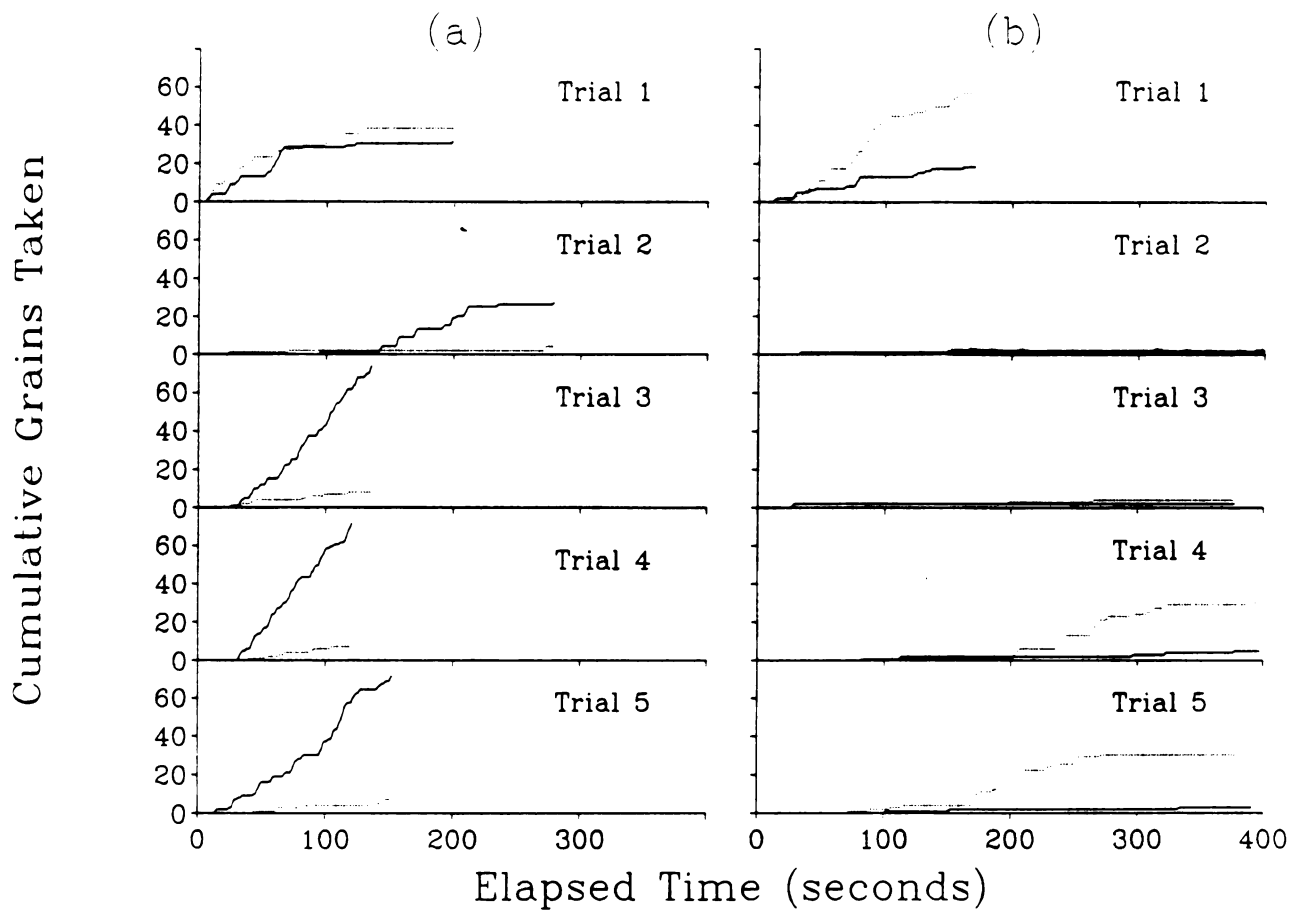
Figure III.5: The typical behavior of two focal chicks in discrimination studies over the course of 5 successive trials. The data presented are the cumulative number of grains taken as a function of time. The dotted line corresponds to orange grains while the solid line corresponds to red. (a) orange grains distasteful; (b) red grains distasteful.

specific quantities that were compared were trial number and $(rate_{orange} - rate_{red})$. A Wilcoxon's signed ranks test revealed a significant difference between trials 2 (the middle trials) and 5 (the final trials) for the quantity $(rate_{orange} - rate_{red})$ in both discrimination experiments (0.05 level). The ability of the chicks to learn which color was distasteful and their associated switch to foraging on the alternate color (as demonstrated statistically) provides evidence that the two colors are distinguishable by the chicks.

A runs test performed on data from the original preference experiments independently suggests that chicks can discriminate orange and red grains. A run is defined as a set of one or more grains of a given color taken in an unbroken sequence. For each focal chick, a t_s value is calculated (Sokal and Rohlf 1981) from the number of observed runs (n_{runs}), and the total number of grains taken of each of the two colors $(n_1$ and $n_2)$.

$$t_s = \frac{n_{runs} - (2n_1n_2)/(n_1 + n_2) - 1}{\sqrt{2n_1n_2(2n_1n_2 - n_1 - n_2)/(n_1 + n_2)^2(n_1 + n_2 - 1)}}$$

The value of t_s is positive if there is an anti-correlation between successive choices and negative if there is a tendency for the grains to be selected in runs. The average calculated from the distribution of t_s values from the 10 focal chicks was compared using a t-test to an average calculated from an expected distribution assuming random selection of the two colors (Figure III.6a and Table III.4). This expected distribution was generated by a computer simulation (refer to Appendix C). There is a significant tendency for the grains to be taken in runs (t-test, 0.05 level). This non-random selection of colors provides further evidence that the chicks are capable of distinguishing between red and orange.
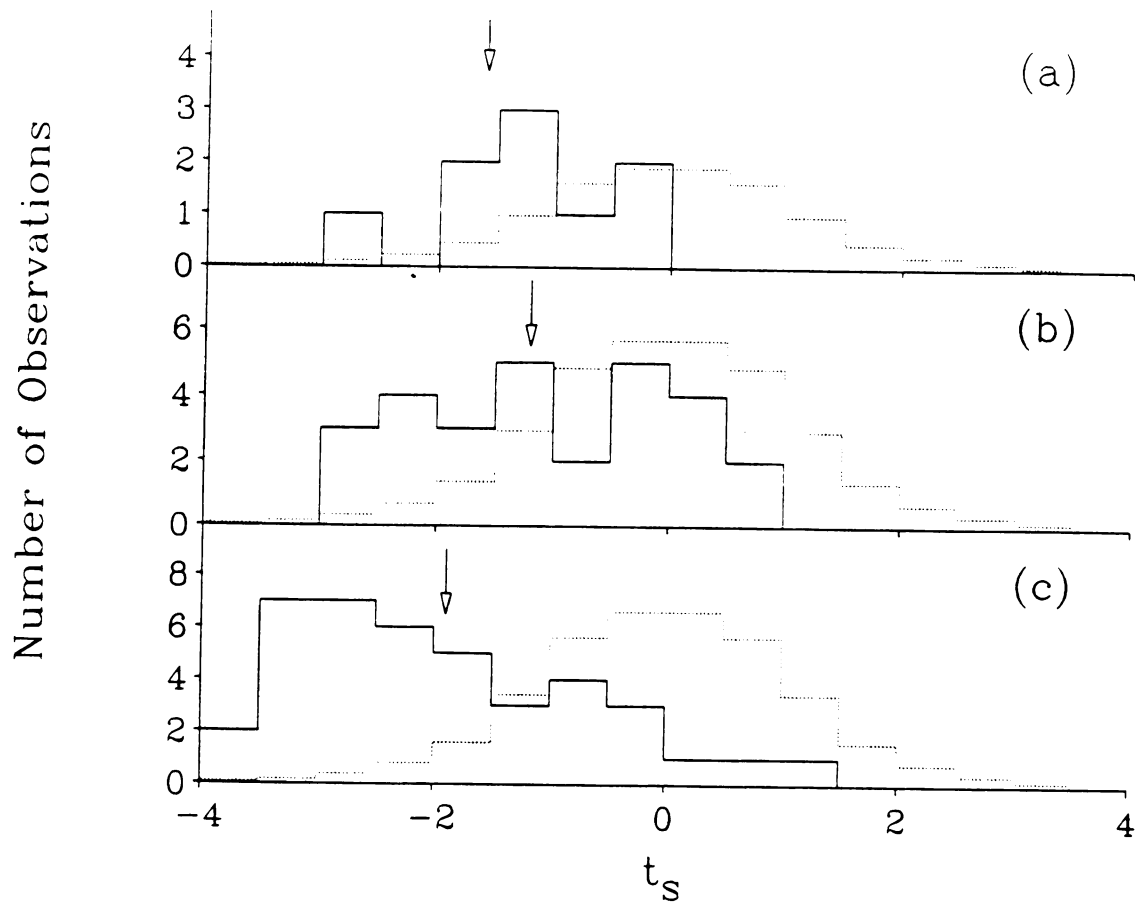
Figure III.6: The distribution of t_s values (solid histograms) from (a) the preference experiment, (b) the cryptic prey experiment with no prior introduction to a prey type, and (c) the cryptic prey experiment with introduction. All experimental distributions are compared to an expected distribution (dotted histograms) generated by a computer simulation. The arrows indicate the average values of the experimental distributions. The mean of the expected distribution is always zero.

Table III.4: The average t_s values in the runs test for the various studies, and the expected values if there were only random selection of grains. A * indicates a significant t-test, 0.05 level.

Test	t_s	$\pm$ S.D.
preference experiment	-1.6	1.3 *
cryptic prey no introduction	-1.2	1.2 *
cryptic prey with introduction	-1.9	1.3 *
expected (random selection)	0.00	0.01

B Experiments with Cryptic Prey

The experiments with cryptic prey test whether a change in an ability to find one cryptic prey type will interfere with the ability to find another equally cryptic type. Figure III.7 displays the behavior of a typical focal chick without a prior introduction to a single prey type, and Figure III.8 displays the behavior of one chick introduced to red grains and one chick introduced to orange grains.   Three ANOVA tests (Tables III.5, III.6, and III.7), one each for no introduction, red introduction, and orange introduction, demonstrated statistically that trial number had no significant effect on the relative rate $(rate_{color1} - rate_{color2})$ at which grains were taken (0.05 level). Therefore, only the first trial was considered in the three subsequent t-tests to compare the mean rates at which each color was chosen (Table III.8). With or without an introduction, the mean rates are not significantly different (t-test, 0.05 level). Thus over the course of a single trial and over three successive trials, there is no indication that specialization develops, hence no indication of interference between prey types.

Figure III.7: Experiments with cryptic prey - no prior introduction: The typical behavior of a focal chick over the course of 3 successive trials. The data presented are the cumulative number of grains taken as a function of time. Orange and red grains were presented against a cryptic background. The dotted line corresponds to orange grains while the solid line corresponds to red.

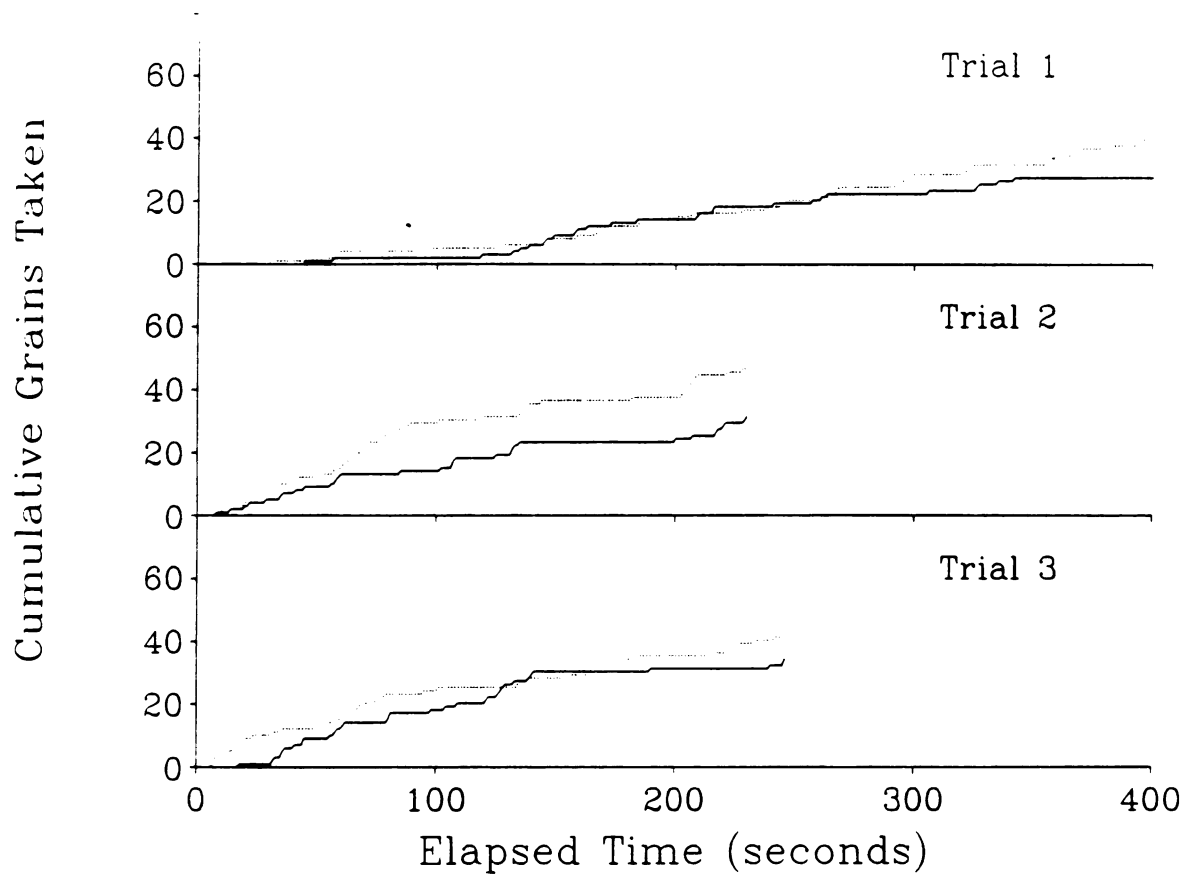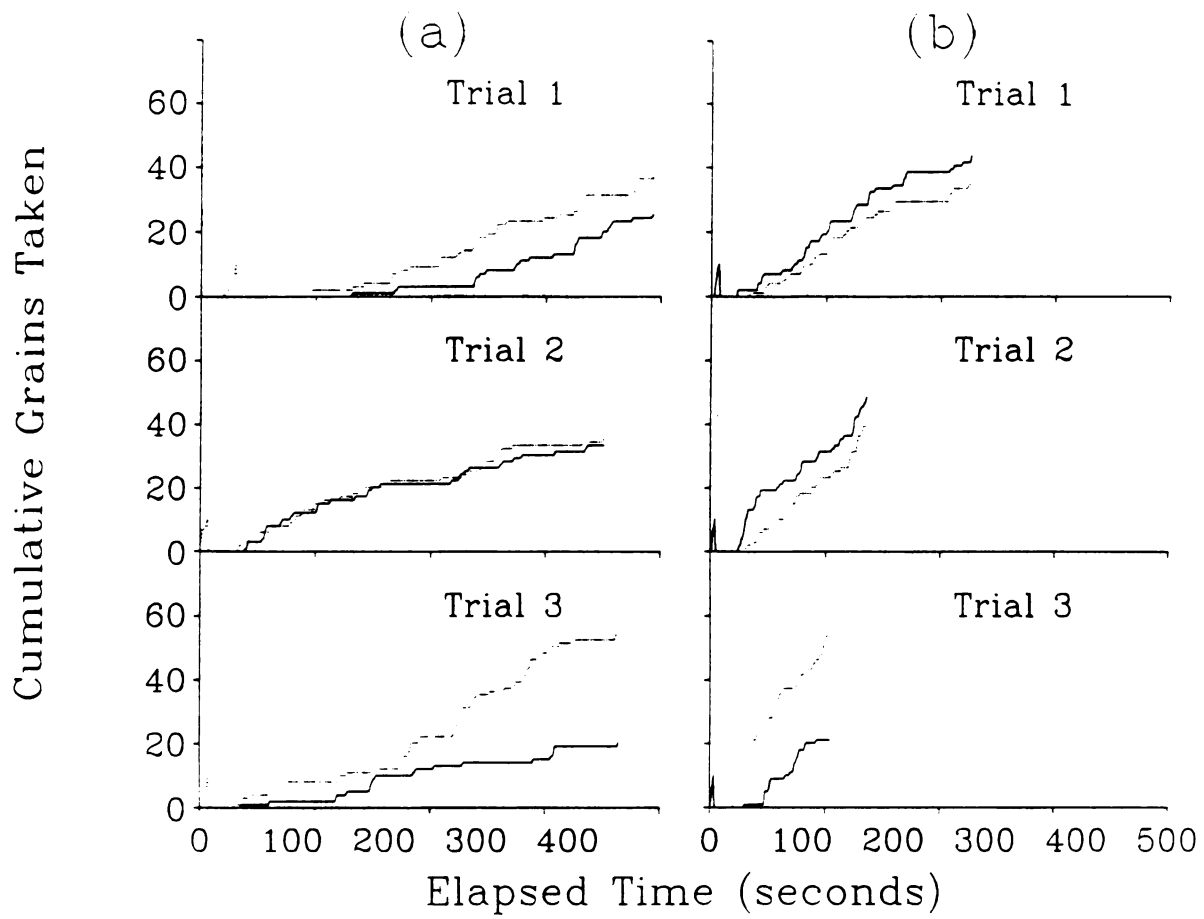Figure III.8: Experiments with cryptic prey - prior introduction: The typical behavior of a two focal chicks over the course of 3 successive trials. Chick (a) was introduced to orange grains while chick (b) was introduced to red. The dotted line corresponds to orange grains while the solid line corresponds to red. The spike near time zero corresponds to the chick picking up introductory grains.

Table III.5: ANOVA table for the experiment with no introduction demonstrating that trial number had no significant effect on the relative rates.

Source	dF	SS	MS = SS/dF
Blocks	9	.027	.003
Treatment	2	.013	.007
Error	18	.093	.005
Total	29	.133	.005

F_{block}	0.59	
F_{treat}	1.28	
$F_{table,block}$ (.05,9,18)	2.46	n.s.
$F_{table,treat}$ (.05,2,18)	3.55	n.s.

Table III.6: ANOVA table for the experiment with orange introduction demonstrating that trial number had no significant effect on the relative rates.

Source	dF	SS	MS = SS/dF
Blocks	5	.063	.013
Treatment	2	.030	.015
Error	10	.089	.009
Total	17	.182	.011

F_{block}	1.41	
F_{treat}	1.70	
$F_{table,block}$ (.05,5,10)	3.33	n.s.
$F_{table,treat}$ (.05,2,10)	4.96	n.s.

Table III.7: ANOVA table for the experiment with red introduction demonstrating that trial number had no significant effect on the relative rates. The * indicates a significant difference at the 0.05 level.

Source	dF	SS	MS = SS/dF
Blocks	5	.406	.081
Treatment	2	.089	.045
Error	10	.153	.015
Total	17	.648	.038

F_{block}	5.31	
F_{treat}	2.93	
$F_{table,block}$ (.05,5,10)	3.33	*
$F_{table,treat}$ (.05,2,10)	4.96	n.s.

Table III.8: Results of t-tests on trial 1 for the three experiments with cryptic prey showing no significant difference between the mean rates at which each color was chosen.

Test	Mean Red Rate Trial 1	Mean Orange Rate Trial 1	t_{trial1}	t_{table}
Cryptic Prey No Introduction	.07 ± .04	.12 ± .08	1.77	2.101 (.05,18)
Cryptic Prey Red Introduction	.12 ± .13	.07 ± .05	1.09	2.228 (.05,10)
Cryptic Prey Orange Introduction	.12 ± .09	.08 ± .04	1.32	2.228 (.05,10)

Runs tests, described previously, provide evidence that there may be interference between prey type over short time spans within trials. The distribution of t_s values calculated for the ten focal chicks in the experiment with no introduction and the twelve focal chicks in the experiment with a prior introduction are compared to the expected distributions assuming random selection of grains (refer to Appendix C) in Figure III.6b and III.6c. Table III.4 gives the average values for the experimental and expected distributions which were compared using a t-test. In both experiments, there is a significant trend for the grains to be selected in runs (t-test, 0.05 level). Since both grains and gravel were well-mixed prior to their distribution into the arena and were mixed further as they were scattered, it was regarded as unlikely that the runs resulted from heterogeneity in either prey distribution or microhabitat. No significant differences between the behavior of males and females were found in any of the experiments with cryptic prey (t-test, 0.05 level).

Chapter IV

DISCUSSION

Allen (1989) cites two ways to distinguish the search rate and search image hypotheses. The first, measuring actual search rates during the course of a trial, would show an increase in search rate in the case of the search image hypothesis and a decrease in the case of the search rate hypothesis. This approach is complicated by the difficulty of separating the parameters that make up search rate. In my experiments, overall rates between experiments cannot be compared either. Although the rate at which chicks foraged was depressed when colored grains were presented on a cryptic background as compared to the rates for presentation on a conspicuous background, and this depression would appear to be evidence for search images, both the search rate and search image hypotheses predict this result. With grains more difficult to find on a cryptic background, the development of a search image would be prolonged (search image hypothesis) or there would be a decrease in search rate (search rate hypothesis).

The goal of this series of experiments was to test for evidence of interference as predicted by the search image hypothesis (Guilford and Dawkins 1987), the second approach cited by Allen (1989). When chicks were presented with orange and red grains on a background colored to make both cryptic, they took the two colors in equal proportions. This result suggests that a chick's ability to detect and capture

one form of cryptic prey does not automatically interfere with its ability to detect another equally cryptic prey type over the course of an entire trial. The same result was obtained when chicks were given prior experience with one of the two prey just prior to experiencing both types together. Interference, therefore, does not appear to be a necessary consequence of learning to forage for cryptic prey over the course of a trial or over consecutive trials, at least when the prey are offered in nearly equal proportions.

The fact that no interference was found over the course of an entire trial does not exclude the possibility that the interference implied by the search image hypothesis would be manifested under different conditions. At least four modifications in my experiments might have revealed evidence of interference. First, the prey types I offered were similar in all respects except color; perhaps some other visual feature, such as size or shape, is more relevant in the development of perceptual specializations. Croze (1970), for example, found some evidence for search image based on shape when presenting crows with cockles and mussels, though it is difficult to separate his results from a simple preference for mussels.

Second, the length of the prior exposure of chicks to a single prey type may need to be longer or the introductory prey may need to be cryptic instead of conspicuous. Den Boer (1971), in a study with a Coal Tit given lengthy prior exposure to the green caterpillar larvae which occurs cryptically in its natural habitat, found that the tit preyed upon the green cryptic larvae almost exclusively when presented with cryptic green and conspicuous yellow prey. However, since only one choice was given in a trial, the aversion for yellow could result from the novelty of the prey item. On the other hand, Croze (1970), cited by Krebs (1973) as the most complete evidence for search images, found that Carrion Crows given lengthy prior experience on 'standard red' mussels chose equal numbers of 'standard red' and 'red-red' mussels when they

were presented together on a cryptic background in equal proportions. Presumably, the crows could tell the difference between the two types based on the fact that they always chose 'standard red' first when a pair of mussels were presented to them. Though no specific mention is made that the two colors were of equal crypticity, their reflectance spectra (Croze 1970, page 46) are quite close. Though Den Boer's study may suggest that lengthy prior exposure could result in search image formation, other studies suggest that a search image can be formed quickly (Croze 1970, Dawkins 1971a,b, Murton 1971).

Third, the chicks I tested encountered the alternative prey types in equal proportions. In this case, the search image hypothesis predicts that a chick could not gain enough prior experience on (and thus an enhanced ability to detect) one color to interfere with its ability to find another. On the other hand, a study by Murton (1971) in support of search images showed that Wood Pigeons offered equal proportions of two seed types at approximately equal crypticity with respect to each other specialized on one seed type or the other. The search rate hypothesis predicts no interference in a chick's ability to choose one color over another no matter what the proportions and thus predicts that the proportions of each color taken should reflect the proportion at which each color was offered (Figure IV.1).

Perhaps, though, chicks would only develop perceptual specializations favoring an extremely common type over an extremely rare type. Indeed, in some formulations of the search image hypothesis (Den Boer 1971, Murton 1971), differences in relative abundance, hence in relative rates of encounter, of alternate prey types are assumed to play a crucial role in the formation of search images. For example, Den Boer (1971) presented Great Tits and Coal Tits with different proportions of green and yellow larvae. The interpretation of the results, however, is confounded by the unequal crypticity of the prey types. The observed ratios of the captured prey can be explained
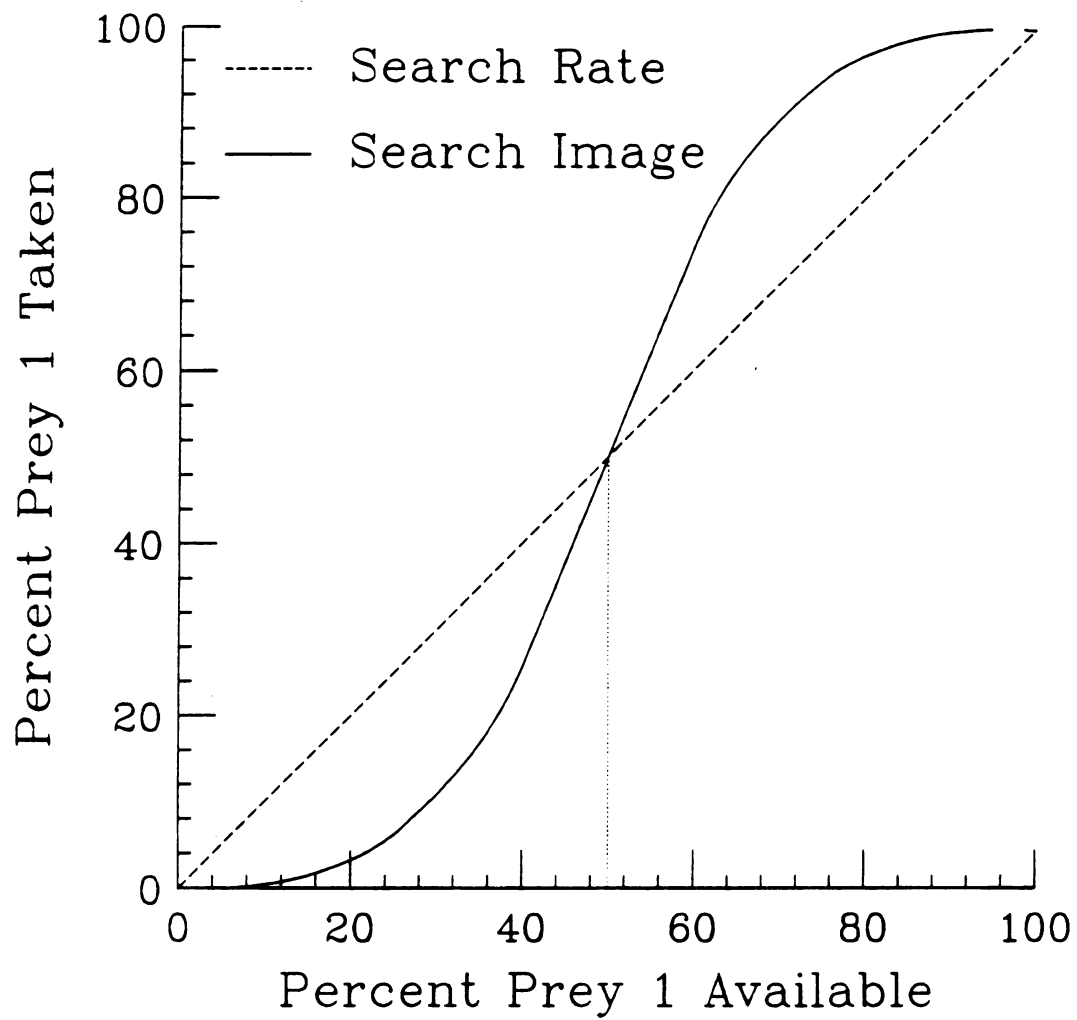
Figure IV.1: Predictions of the search image model and the search rate model as a function of the relative densities of the two cryptic prey species.

entirely based on differences in detection efficiency. Murton (1971) presented Wood Pigeons with different proportions of supposedly equally cryptic tic beans and maple peas and found that the birds had a significant tendency to prey almost exclusively on tic beans. Once again, the interpretation of the results is confounded by the failure to control for equal preference and equal crypticity for the two prey types.

Finally, this experimental approach might have yielded evidence of perceptual specialization if applied in a more naturalistic context to a species more certain to have been under strong natural selection to exploit cryptic prey.

Although the experiments revealed no evidence of interference over the duration of entire foraging bouts, evidence for a temporary form of interference is suggested by the results of the runs tests, which showed that the choice of grain color has some dependence on previous choices. This result can not be fully explained by the search rate hypothesis, and may indicate the formation of a short-lived search image.

These short-term specializations expressed as runs on a specific prey type must make a local impact on the relative abundance of different prey types in order to contribute to apostatic selection. For example, if the predator runs only on one prey type or for a significantly longer period of time on one prey type during the time spent in a patch, the overall effect would be selection against that type.

It is important to stress the value of this approach for further studies of the search image hypothesis. Of previous laboratory studies on search images, only that of Pietrewicz and Kamil (1979, 1981) has presented predators with two cryptic prey types and is, therefore, directly comparable to this study. However, in their study, the two prey types used were not of equal crypticity. In addition, the prey were presented as photographic images on successive slides and not as food items that could be eaten on being recognized as such. This complicates the relationship between performance

accuracy and response time to a stimulus since the birds must also learn about the experimental setup. These latter two points have enabled Guilford and Dawkins (1987) to reinterpret the data using the search rate hypothesis.

Certain of the more naturalistic studies reviewed by Krebs (1973) did incorporate the approach of using more than one prey type, though these studies also have their shortcomings. Not only can Croze's work (1970) be explained using the search image hypothesis, but the search rate hypothesis can be applied as well. For example, when crows were presented with red and black mussels, the birds first took all the red mussels and then all the black mussels (Croze 1971, page 40). Croze interprets this as evidence for search images. But, since red mussels are more conspicuous then black ones, the search rate hypothesis would predict that the search rate would be set by the red mussels. Black mussels would be overlooked. Krebs (1973) criticizes Murton's work (1971) on the basis that individual birds could have specific seed preferences. At the same time, he states that since independent flocks of pigeons did not exhibit exactly the same behavior, individual seed preferences are unlikely. Den Boer's study (1971) has the two problems previously mentioned. In the experiments without prior exposure, there is unequal crypticity of the prey types, and in the experiments with prior exposure, there is the issue of novelty.

Controlled experiments similar to those outlined in the present work, but performed at proportions of prey types other than 50:50, would isolate the question of interference from the search rate hypothesis and would lead to a better understanding of the role of interference in predator behavior. In particular, controls for preference and crypticity would eliminate many of the problems found in previous studies. Finally, similarly controlled experiments should be extended to naturalistic systems in order to reduce the problems associated with the artificiality of behavior in a laboratory system.

Appendix A

Data Conversion Program

```
        program timer
c  this program will create a time file for each experimental
c  run
        real time1,time2
        integer status,icount
        character ctime*32,title*80,filename*80,input*1

        type *,' Please input a title for this run.'
        accept 10,title
10      format(a)
        encode(20,20,filename)
20      format(a14,'.dat')
        open(10,file=title,form='formatted',status='new')
        type *,' Hit <CR> to start to run, and then hit <CR>
1           for every strike.'
        type *,'                To finish the run, type E'
        accept 10,input
        type *,'    The run has been started.'
        call lib$init_timer
        time1=secnds(0.)
        icount=0
30      accept 10,input
        if(input.eq.'E'.or.input.eq.'e')then
            time2=secnds(0.)
            type *,' Test ended at ',(time2-time1),' seconds'
            write(10,*)' Test ended at ',(time2-time1),' seconds'
            go to 90
        end if
        time2=secnds(0.)
        icount=icount+1
        type *,' Event Number : ',icount,'      Elapsed Time : '
1           ,(time2-time1)
        write(10,40)icount,(time2-time1)
40      format(i6,f10.4)
c       call lib$show_timer(,2)
        go to 30
90      end
```

```
        subroutine title_read(title,argument)
        character title*1
        integer argument
        dimension title(32)
        type 11,title
11      format(a)
        type *,' Argument=',argument
        return
        end
```

Appendix B

Asymmetry Value Simulation

```
        program CoinFlips
c  This program randomly flips a coin a given
c  number of times, and
c  then determines the asymmetry parameter.
        implicit none
        integer iseed,i,j,k,Mat(10),Ntrials,Nflips
        real Nh,Nt,AP,rnd

10      type *,' Please input a random seed.'
        accept *,iseed
        type *,' Input Number of trials'
        accept *,Ntrials
        type *,' Input Number of flips per trial'
        accept *,Nflips
        do i=1,Ntrials
          Nt=0
          Nh=0
          do j=1,Nflips
            rnd=ran(iseed)
            if(rnd.gt.0.5)then
                Nh=Nh+1
              else
                Nt=Nt+1
            end if
          end do
          Ap=0
          if(Nh.gt.Nt)AP=(Nh-Nt)/Nh
          if(Nh.lt.Nt)AP=(Nt-Nh)/Nt
          k=int(10.0*Ap)+1
          if(k.gt.10)k=10
          mat(k)=mat(k)+1
        end do
        do k=1,10
          type *,mat(k)
          mat(k)=0
        end do
        go to 10
        end
```

Appendix C

Runs Test Simulation

```
        program CoinFlips2
c  This program randomly flips a coin a given number
c  of times, and then determine the number of runs
c  in the sample.  The probability of getting a .true.
c  is not equal to the probability of getting a
c  .false.
        implicit none
        integer iseed,i,j,k,Mat(-20:20),Ntrials,Nflips
        real Nh,Nt,AP,rnd,runs,H,T,Ts,prob,Num,Dem
        logical list(100)

10      type *,' Please input a random seed.'
        accept *,iseed
        type *,' Input Number of trials'
        accept *,Ntrials
        if(Ntrials.eq.0)go to 99
        type *,' Input Number of Heads and number of Tails.'
        accept *,H,T
        Nflips=H+T
        Prob=H/float(Nflips)
        do i=1,Ntrials
          Nt=0
          Nh=0
          do j=1,Nflips
            rnd=ran(iseed)
            if(rnd.gt.Prob)then
                Nh=Nh+1
                list(j)=.true.
              else
                Nt=Nt+1
                list(j)=.false.
            end if
          end do
          runs=1
          do j=2,Nflips
            if(List(j-1).ne.List(j))Runs=Runs+1
          end do
c         type *,' N1 ',Nh,'      N2 ',Nt,'      Runs ',Runs
          Num=(runs-((2*Nt*Nh)/(Nt+Nh))-1)
          Dem=sqrt(2*Nt*Nh*(2*Nt*Nh-Nt-Nh)/
     1            ((Nt+Nh)**2*(Nt+Nh-1)))
```

```
      Ts=Num/Dem
      k=nint(10.0*Ts)
      if(k.gt.20)k=20
      if(k.lt.-20)k=-20
      mat(k)=mat(k)+1
   end do
   do k=-20,20
      type *,float(k)/10,mat(k)
   end do
   go to 10
99 do k=-20,20
      write(99,*)float(k)/10,mat(k)
   end do
   end
```
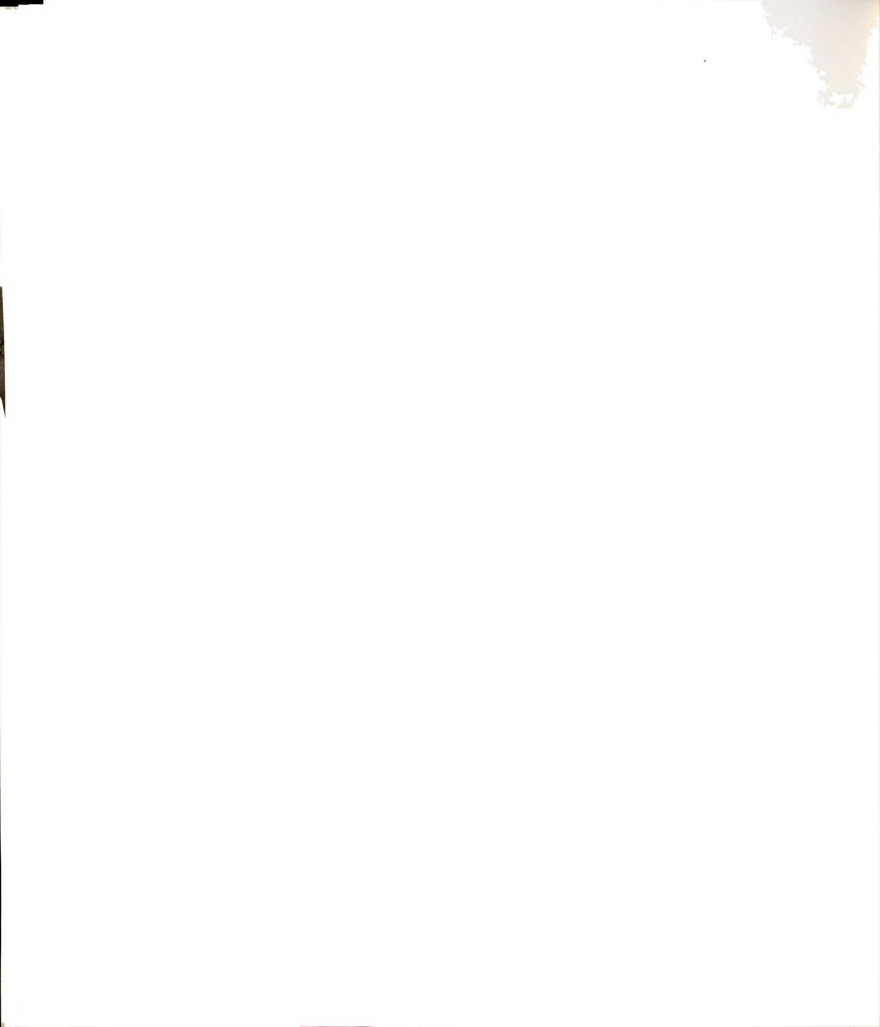
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