

1983

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I wish to thank D. A. Riley, R. G. Cook, M. R. Lamb, and S. J. Spengler for advice, encouragement, and critical discussion throughout the course of this research. Funds for this study were provided by a postdoctoral fellowship from the National Institute of Mental Health (NIMH). Additional funding was provided by NIMH Grant MH22153 and National Science Foundation Grant BNS7908839 to D. A. Riley.

Submitted June 8, 1982; revised November 8, 1982.

# Visual Search and Selection of Natural Stimuli in the Pigeon: The Attention Threshold Hypothesis

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## Abstract

During visual search for samples of varying proportions of familiar, natural food grains displayed against a complex gravel background, pigeons exhibited “matching selection,” a tendency to overselect the more common grain. The matching selection effect was decreased at low levels of stimulus/background contrast and reversed when the grains were highly conspicuous. The results were consistent with the hypothesis that stimulus detectability should be enhanced by recent experience with a particular grain type, but they showed no convincing indications of a corresponding effect on the response criterion. An explanatory model, termed the *attention threshold* hypothesis, argues that the mean latency of discovery can be minimized by selectively attending to one stimulus type at a time and switching to a more generally receptive state when the rate of discovery falls below a threshold value. The model appears to account for the fact that the response rate was highest toward samples containing a single grain type and decreased as the relative proportions approached equality. Additional consequences of the adoption of this theoretical perspective were explored in some detail. Among other results, the evidence suggests that the switching threshold might be chosen so as to optimize the rate of food discovery.

Animals that are ecological generalists, that is, animals that forage for a variety of food, commonly exhibit a selection bias that depends on relative frequency (Curio, 1976; Krebs, 1973). Food types uncommon in the environment tend to be disproportionately underrepresented in the diet, whereas more abundant foods are consumed in excess. A selection bias could result from a number of passive factors, such as heterogeneity in the spatial distribution of food types or changes in food accessibility with density (Murdoch & Oaten, 1974). In animals that conduct a visual search for food, however, Tinbergen (1960) hypothesized that the bias may be attributable to active processes. Recent experience with a particular food type, he argued, should increase the likelihood of a similar, subsequent discovery, relative to the experience of encountering food of a disparate appearance. Because the essential feature of this process is a tendency to match or

repeat immediately previous feeding acts, a bias in favor of more frequent food types will be referred to as “matching selection.” Similarly, “oddity selection” constitutes a tendency to concentrate on rarer food types and to take disproportionately fewer of the common ones.

Processes capable of generating a matching selection bias appear to fall into two general categories. In the first case, the bias results mainly from preferential responding to food-related stimuli in accordance with the prior history of reward. Feeding responses for which the animal has been rewarded most often or most recently will tend to occur with a higher probability, thereby amplifying the frequency of selection of relatively abundant food types.

In contrast, Tinbergen termed his hypothetical process *hunting by searching image* after von Uexküll’s (1957) anecdotal description of the ef-

fects of expectancy on visual perception and clearly intended that it be understood to involve a perceptual change, rather than simply an effect of response contingencies. The bias in this case is assumed to reflect an improvement in the animal's ability to discriminate food-related stimuli from a background containing features of a similar appearance. Cryptic stimuli that are detected more often or more recently are assumed to be more readily discriminated than those with which the animal has had less experience, thereby assuring a higher frequency of selection for relatively abundant food types. Subsequent researchers (Croze, 1970; Dawkins, 1971a; Krebs, 1973; Pietrewicz & Kamil, 1977, 1979) have interpreted Tinbergen's perceptual change as an attentional process, conceivably involving both discrimination learning and shifts in selective attention among alternative food stimuli.

The literature on the occurrence of such perceptual phenomena in animals deals primarily with simple, artificial stimuli, such as shapes, colors, or line orientations (Riley & Leith, 1976; Sutherland & Mackintosh, 1971), but a number of workers have observed analogous effects with more complex, natural stimuli. Dawkins (1971a) demonstrated discrimination learning and something akin to overshadowing in chicks feeding on colored rice grains scattered over a matching pebble background. She has also obtained evidence of transitory attentional states in the same preparation (Dawkins, 1971b). Using photographs of cryptically colored moths as stimuli in an operant conditioning paradigm, Pietrewicz and Kamil (1977, 1979) found indications of increases in discriminability associated with runs in the imposed sequence of stimuli in blue jays. The results are similar to those found in investigations of the repetition effect in human visual-choice tasks (Rabbitt, Cumming, & Vyas, 1977). The bearing of this work on Tinbergen's original hypothesis is only indirect, however. In none of these studies has the perceptual mechanism been causally linked to the occurrence of matching selection.

On the other hand, the numerous studies in which matching selection has actually been demonstrated have seldom been concerned with elucidating the

underlying behavioral mechanism. It is not surprising, therefore, that the source of the selective bias is often difficult to adduce. Those studies that entail the deliberate introduction of a bias via pretraining on one stimulus type (Allen & Clarke, 1968) or that entail the first exposure to novel, conspicuous stimuli (Fullick & Greenwood, 1979; Willis, McEwan, Greenwood, & Elton, 1980) are probably most parsimoniously interpreted as elicitations of response biases. Other studies may be consistent with a perceptual bias, but because stimulus discriminability was not explicitly manipulated, the design cannot fully exclude alternative inferences (Allen, 1972; Cook & Miller, 1977; Manly, Miller, & Cook, 1972).

Although the source of the bias in matching selection is difficult to demonstrate directly, there are circumstances that would clearly favor a perceptual account. For example, a bias generated by an attentional process ought to be demonstrable even during selection among familiar stimuli that have been equally associated with reward. A perceptual bias should also be predictably affected by the relative discriminability of the stimuli. For conspicuous stimuli, that is, those that contrast strongly with the background on at least one dimension, response latency should be limited mainly by the animal's visual resolution and scanning speed, and attentional influences on detection rate should be minimal. The relative advantage of a search for a limited subset of stimulus attributes should initially tend to increase with the degree of resemblance between stimulus and background and yield an increase in the magnitude of the selection bias. This effect of stimulus discriminability cannot be monotonic, however. As the food stimuli approach mimesis, providing a near match to some elements of the background, even a rigorous stimulus selection will not significantly enhance the animal's discriminative performance. Matching selection resulting from a perceptual bias should, thus, be most apparent at an intermediate level of crypticity, with stimuli that resemble the background, but which are unlikely to be confused with it.

On the other hand, because a response bias depends only on the relative densities of the food

types, it is conceivable that it would operate without regard to the background against which the stimuli were presented. Alternatively, because the magnitude of a response bias is strongly affected by the rate of reward, matching selection resulting only from response contingencies might be more evident for the most conspicuous stimuli where the feeding rate is maximized. In either case, the two types of process appear to make different predictions for the outcome of manipulating the discriminability of the food stimuli. It should be possible, therefore, to test for the occurrence of a perceptual bias in a free-response system by quantification of the intensity of matching selection at varying degrees of stimulus conspicuousness.

The domestic pigeon is, for a variety of reasons, an ideal species with which to test these hypotheses. Evidence from matching-to-sample studies (Riley & Roitblat, 1978) and research on visual search for computer-generated targets (Blough, 1979) suggest that pigeons exhibit many of the perceptual effects that are associated with selective attention in humans. Pigeons are ecological generalists, feeding in flocks on the ground on a large diversity of cereals, legumes, and weed seeds (Murton & Westwood, 1966). There is also good inferential evidence of matching selection in pigeons feeding on natural food grains in the field (Murton, 1971).

The experimental design involved presenting domestic pigeons with an array of familiar, natural food grains scattered at random over a visually complex gravel background. In the first experiment, two different stimulus sets, each consisting of a pair of grain types that were dissimilar in appearance but roughly equivalent in detectability, were presented on two types of backgrounds to determine the relationship between matching selection and stimulus conspicuousness. An explanatory model was then proposed that accounted for the results in terms of a time-dependent switching process among several attentional states. In the second experiment, the most effective stimulus combination was presented over a wide range of relative proportions to explore the consequences of the adoption of the model perspective.

## Experiment 1

### Method

#### *Subjects*

Three experimentally naive Silver King pigeons, one cock (Bird 70) and two hens (Birds 12 and 20), were used in these experiments. They were maintained in individual cages at 75-80% of their free-feeding weight.

#### *Apparatus*

*Backgrounds.* The background consisted of No. 2-grade beach gravel that had been run through a 7-mm mesh screen to remove large pieces and then picked over to eliminate shells, glass chips, and pieces of brick and pottery. Cleaned gravel (500 cc) was mixed thoroughly with about 80 cc of water-clear casting resin and poured into an opaque plastic pan, 22.4 cm wide  $\times$  14.8 cm long  $\times$  4.3 cm deep. The mixture was spread evenly to a depth of about 1 cm and allowed to harden. Three coats of clear, satin-finish Varathane were subsequently applied to the surface. The final result was a hard, glossy surface, with a particle size of between 2 and 7 mm. The predominant color was yellow-orange, but there were large components of black, red-brown, tan, and creamy or translucent white grains. The background was very rough, with as much as 8-10 mm of relief between the height of peaks and troughs. A total of 20 pans containing this "mixed" background was prepared. Another 20 pans were treated similarly, but instead of clear Varathane, they were given two coats of machine-gray spray enamel, followed by a light coat of gloss white, which produced a uniform, pale-gray surface against which all of the experimental stimuli were readily visible. In subsequent reference, this will be termed the *gray* background.

*Stimuli.* The stimuli used were two species of oriental bean and two types of domestic wheat. They are all grains of the sort that are fed on readily by pigeons in their native habitat (Goodwin, 1967; Murton & Westwood, 1966). They bear little resemblance to one another, other than in general size. In pilot tests, human subjects found all of them difficult to discriminate from the mixed gravel background, but the two grains in Stimulus Set 1 (SS1) appeared to be consistently harder to detect than those grains in Stimulus Set 2 (SS2). Minor manipulations of reflectance and orientation were used to enhance this difference.

SS1 consisted of moth beans and pearled wheat. Moth beans, *Phaseolus aconitifolius* Jacq., are smooth and cylindrical, roughly 2.3  $\times$  4.0 mm, and uniform in color, ranging from pale tan to reddish brown. Pearled wheat, *Triticum aestivum* L., is soft yellow wheat from which the pericarp, or outer seed coat, has been ground away. The seeds are ovoid, about 2.5  $\times$  5.0 mm, yellowish white, and translucent, grading to opaque at the ends. They were invariably placed in the pans with the conspicuous ventral furrow downwards and concealed from view. Both grain types in SS1 were coated with a thin layer of petroleum jelly prior to use to enhance their specular reflectance and increase their resemblance to the plastic coated

gravel. Tests using coated and uncoated grain confirmed that the petroleum jelly did not inhibit feeding.

SS2 consisted of black gram and red wheat. Black gram, *Phaseolus mungo* L., are roughly rectangular or cylindrical beans, about  $3.3 \times 3.8$  mm. They are dark brown to black with a dull surface and a conspicuous white hilum, or attachment mark, on the ventral side. In the pans, the black gram was placed with the hilum up and clearly visible to the birds. Grains of hard red wheat, *Triticum durum* Desf., are ovoid or spindle-shaped, roughly  $2.8 \times 6.5$  mm, and dull reddish brown, grading to yellow at the ends. The conspicuous ventral furrow was always oriented downward in the pans, but the exposed side of the seed bears a characteristic mark at its base, which corresponds to the position of the embryo, that at least subjectively appears to enhance its conspicuousness.

*Stimulus positioning.* For each trial, a sample of 20 grains of one of the two stimulus sets in some predetermined relative proportion was distributed over the surface of one of the pans. To insure that the feeding behavior would be free of spatial artifacts, the grains were placed in the pans one at a time, at independently determined random locations. A minimum spacing of 1.5 cm was maintained between adjacent grains to reduce the likelihood of multiple, simultaneous discoveries. When this spacing on the mixed background was used, human subjects were seldom able to detect more than one grain at a time.

#### Procedure

*Training.* To insure thorough familiarity with the stimulus grains, the birds were fed the four experimental seed types for 1 month as a supplement to their usual pigeon food mix; the supplement constituted roughly 40% of their daily ration. They were given long, daily exposures to the apparatus to become habituated to the room, the experimenter, and the abrupt removal of the pan that terminated feeding. For an additional 2 wk., the birds' entire daily grain ration came from the four experimental seed types presented against the mixed and gray backgrounds in the apparatus. The birds were trained to maximum speed by gradually reducing the time allotted for feeding and were considered ready for testing when they could detect and remove 16 of the 20 grains of a 50:50 mixture of either stimulus set against a mixed gravel background within 10 sec.

*Testing.* The birds were placed in an opaque chamber, 47 cm on a side, with a window cut in the center of one wall, 8 cm wide  $\times$  17 cm high, at a height of 8 cm from the chamber floor. The dimensions of the window were large enough to admit the full range of movement of the bird's head and neck but prevented it from climbing out into the pan. At the start of each trial, the stimulus pan was centered below the window, with the edge of the lip even with the sill. Whenever the experimenter approached the chamber to remove or replace a pan, the bird would invariably back off into the chamber, returning to the window only when the experimenter moved away. Timing was initiated when the bird's head passed through the plane of the window and was terminated when a criterion number of pecks had been taken. The criterion, derived empir-

ically during the training sessions, was that number of pecks that a given bird required to remove, on the average, 10 of the 20 grains in the pan. The criterion varied from 12 to 17 pecks among the three birds. At the end of the trial, the experimenter approached the window, the bird stopped feeding and backed away, and the pan was removed for analysis. The duration of the trial, the number of pecks taken, and the number of grains of each type consumed were recorded.

#### Design

Each bird was given one session per day, consisting of 10 trials of a single combination of stimulus set (SS1 or SS2), background (gray or mixed), and relative proportion (20%, 50%, or 80% beans). No more than 15 sec elapsed between trials within a session. All 12 possible treatment combinations were applied in randomized order, with the constraint that the same stimulus set was not to be used with a given bird for 2 days in succession. Selection and sequence of pans used was also fully randomized. The experiment was repeated three times, for a total of 30 trials for each subject on each treatment combination.

## Results

### *Analysis of Task Difficulty*

By taking ratios of the single-trial measures, feeding behavior was divided into a searching component, represented by the peck rate (number of pecks/trial duration) and a handling component, represented by the peck accuracy (number of grains taken/ number of pecks). The relative difficulty of the different tasks was assayed with a three-way analysis of variance (ANOVA; Background  $\times$  Stimulus Type  $\times$  Relative Proportion) on the ratio variables, conducted on data from each subject independently, as well as on pooled results from all three birds. The *F* statistics provided in the text are those from the pooled test. No effect in the pooled sample was accepted as significant, however, unless it could be shown to be significant in the individual tests for at least two of the three birds as well, and congruent in direction if not significance, for the third bird. Mean values for each ratio for each combination of treatment conditions are displayed in Tables 1 and 2.

The peck rate was significantly higher against the gray background than against the mixed,  $F(1, 1068) = 521, p < .001$ , and higher toward SS2 than SS1,  $F(1, 1068) = 27.6, p < .001$ . The difference between gray and mixed backgrounds was larger for SS1 than for

SS2,  $F(1, 1068) = 14.1, p < .001$ , primarily because of a significantly greater depression of rate against the mixed background. For the gray background alone, the rates for the two stimulus sets did not differ, ( $p > .05$ , using Scheffé's method of multiple contrasts). The peck rate was consistently lower for samples containing a 50:50 mix of grain types,  $F(2,1068) = 10.4, p < .001$ . This effect of relative proportion was somewhat stronger for SS2 than for SS1,  $F(2, 1068) = 7.33, p < .001$ , but was not significantly affected by the background,  $F(2, 1068) = 1.05, p > .3$ . The direction of these relationships held true for each bird individually as well, though there were differences between birds in the magnitude and significance of the effects.

There was a significant main effect of stimulus set on accuracy, with pecks to SS2 being more accurate,  $F(1, 1068) = 71.4, p < .001$ . There was no main effect of background on accuracy,  $F(1, 1068) = 2.50, p > .1$ , but there was a significant Background  $\times$  Stimulus Set interaction,  $F(1, 1068) = 20.6, p < .001$ . The interaction was apparently attributable to the effect of background on accuracy for SS1; accuracy on SS2 was not significantly affected by background ( $p > .05$ , using Scheffé's method of multiple contrasts). Accuracy was significantly higher for samples containing 80% beans,  $F(2, 1068) = 9.21, p < .001$ , but there were no significant interaction effects involving the relative proportion factor. All effects were consistent in direction and magnitude across subjects.

**Table 1.** Response Rate (Pecks/Sec)

Treatment	Proportion of beans			
	20%	50%	80%	Pooled
Gray background				
SS1	2.88	2.83	2.89	2.87 <sup>a</sup>
SS2	2.93	2.77	3.01	2.90 <sup>a</sup>
Mixed gravel background				
SS1	2.28	2.21	2.16	2.22 <sup>b</sup>
SS2	2.49	2.30	2.52	2.44 <sup>c</sup>

Means that do not share a common superscript were significantly different ( $p < .05$ , Scheffé's method of multiple contrasts). SS1 = Stimulus Set 1, SS2 = Stimulus Set 2.

### Analysis of the Selection Bias

The difference between the number of beans removed during a set of feeding trials and the number that would have been expected from a random selection process provides a qualitative measure of the selection bias for each treatment combination. The deviation values, displayed in Table 3, were each computed from the results of 90 feeding trials, with 20 grains presented per trial, for a total of 1800 grains. The total number of grains of both kinds consumed in these trials is also listed. There is a clear suggestion of matching selection, with negative deviations for the 20% treatment and positive deviations for the 80% treatment, only; for SS2 on the mixed background. The significance of the differences between treatments is difficult to assess by this means, however. Quantitative analysis requires a more derived measure, one that summarizes the direction and magnitude of the selection bias across all three relative proportion treatments.

Manly et al.'s (1972) measure,  $\alpha$ , provides an indication of the mean discrepancy between the proportion of a given grain in the sample presented and the proportion actually consumed. It is calculated as

$$\alpha = \ln(B/b)/\ln(A/a)'$$

in which  $A$  and  $B$  represent the number of grains of each type in the sample, and  $a$  and  $b$  are the number remaining after a trial. When a value for  $\alpha$  is ob-

**Table 2.** Response Accuracy (Grains/Peck)

Treatment	Proportion of beans			
	20%	50%	80%	Pooled
Gray background				
SS1	.656	.645	.688	.663 <sup>a</sup>
SS2	.672	.683	.754	.703 <sup>ab</sup>
Mixed gravel background				
SS1	.617	.578	.611	.602 <sup>c</sup>
SS2	.698	.733	.765	.732 <sup>b</sup>

Means that do not share a common superscript were significantly different ( $p < .05$ ; Scheffé's method of multiple contrasts). SS1 = Stimulus Set 1, SS2 = Stimulus Set 2.

tained for each treatment in a range of relative proportions, it is approximately log-linearly related to the proportion of *A* grains (in this case, beans) in the sample. The slope of the regression line of  $\ln a$  against proportion of beans, called the "selection index," provides a summary measure of the direction and intensity of selection, with negative slope values indicating matching selection and positive values indicating oddity selection.

Because the combination of ratio and logarithmic operations tends to inflate the variance, it is generally better to use mean values of  $a$  and  $b$  taken over several trials. In this case, the mean number of each grain type remaining over the 10 trials in a single session was used to compute each value of  $a$ . There were, therefore, three measures of  $a$  for each combination of background, stimulus set, and relative proportion for each bird. The pooled selection index from each combination of treatment conditions is listed in Table 3.

To determine the effect of the task parameters on the selection bias, the values of  $\ln a$  were subjected to a three-way ANOVA (Background  $\times$  Stimulus Set  $\times$  Relative Proportion), which employed weighted orthogonal polynomials for contrasts involving the third factor. Because the selection index is expressed in the slope of  $\ln a$  on the relative proportion, the effects of concern were only those

that included interactions with the first, or linear, component of the proportion factor. There was a significant main effect of background on selection intensity,  $F(1, 96) = 56.6$ ,  $p < .001$ , with matching selection appearing only against the mixed background and oddity selection appearing against the gray background. A significant Background  $\times$  Stimulus Set interaction,  $F(1, 96) = 16.27$ ,  $p < .001$ , reflected a much greater intensity of matching selection on the mixed background for SS2. There were only minor differences in the magnitude of the effects across birds.

## Discussion

The gray-enameled background offered little hindrance to perception or handling of either stimulus set. The response rate for all three birds was maximized under this treatment: The mean interpeck interval was about 340 msec. Because the physical movements of pecking and swallowing alone require 250-350 msec to complete (Zeigler, 1976), the scanning time for the discovery of the next grain must have been negligible. There is also no compelling evidence for the occurrence of false alarms on the gray background. The low levels of response accuracy observed in these birds (Table 2) were equally evident in their home cages and

**Table 3.** Deviation From a Random Expectation of Number of Beans Taken

Treatment	Proportion of beans						Selection index
	20%		50%		80%		
	Deviation	Total grains	Deviation	Total grains	Deviation	Total grains	
Gray background							
SS1	7.2	874	-16.0	928	-21.4	918	.517 <sup>a</sup>
SS2	49.2	884	50.5	927	1.8	919	.940 <sup>a</sup>
Mixed gravel background							
SS1	-36.2	911	-16.5	837	4.4	922	-.656 <sup>b</sup>
SS2	-92.4	897	30.5	945	68.2	936	-3.006 <sup>c</sup>

Values that do not share a common superscript were significantly different ( $p < .05$ , using Scheffé's method of multiple contrasts). Slope estimates for all treatments were significantly different from zero ( $p < .02$ ). For each treatment combination, the table lists the deviation of the number of beans consumed from a random expectation and the total number of grains of both types taken. SS1 = Stimulus Set 1, SS2 = Stimulus Set 2.

are apparently attributable more to inefficiency in grasping and manipulating the grains than to mistaken responses to the painted gravel.

The natural, mixed background, on the other hand, appears to have interfered substantially with a visual search for grain. The response rate was lower on the mixed background than on the gray, with interpeck intervals that were perceptibly longer than the time required to produce a peck response. The difference presumably reflects an increase in the time required to scan the display and locate each successive food item, which implies that both sets of stimuli were more difficult to perceive against this background. The degree of crypticity was not equivalent in the two sets, however: The depression in the response rate was larger for SS1 than for SS2. In addition, the response accuracy for SS2 was not altered by presenting the grains against the mixed background, whereas that for SS1 was significantly lower in the mixed background treatment, which suggested a higher error rate and, by inference, a higher rate of false alarms.

Given these results, the hypothesis of a perceptual bias predicts no matching selection against the gray background. Within the mixed-background treatments, it predicts that matching selection will be more evident for SS2 than for SS1. Each of these predictions was borne out in the analysis (Table 3). Because a response-bias model cannot readily account for this pattern of effects, the results seem most cogently interpreted as the consequence of a perceptual bias. Several naturalistic studies of visual search in other bird species have noted that the matching selection effect is reduced or even eliminated at high food densities (Allen, 1972; Cook & Miller, 1977), and Cook and Miller (1977) have seen evidence of a decline at low densities, as well. If differences in food density can be considered as comparable to differences in crypticity, in that they have similar effects on the rate of stimulus discovery, these results parallel those of the present study.

The occurrence of a weak but consistent oddity selection in the conspicuous treatments was not directly predictable from either hypothesis. It could conceivably have resulted from an effort to reduce response competition, assuming that the birds were

in fact identifying or categorizing each stimulus prior to making a response rather than merely pecking unselectively at any contrasting stimulus. When stimuli are selected from a mixed array in homogeneous runs of a single type, the rest of the array can be treated as components of the background, thereby reducing interference and increasing the rate of stimulus processing (Bond, 1982). The greater the disparity in the relative densities of the stimulus types, the easier it may be to consider the more common stimulus as a component of the background. This would account not only for the occurrence of oddity selection, but also for the reduction in response rate observed when the animals were feeding on equal numbers of the two kinds of grain (Table 1).

In the only previous investigation of oddity selection in the pigeon, Zentall, Hogan, and Edwards (1980) tested whether their birds exhibited an inherent bias toward selection of the odd panel in a 25-panel display, even when all responses were equally rewarded. They found a weak indication of oddity selection, which they attributed to the birds' preference for particular stimulus colors. No pecks directed at any part of the display went unrewarded, however, and this may have served to eliminate the need to categorize target stimuli, thereby eliminating the oddity selection effect. When unrewarded background stimuli of a contrasting appearance have been employed, as in several studies on other species, oddity selection has commonly been observed in the response of animals to conspicuous visual targets (Bond, 1982; Mueller, 1974, 1975; Ohguchi, 1978; Ruggiero, Cheney, & Knowlton, 1979).

#### The Attention Threshold Hypothesis

The concept of a searching image has been predominantly referred to in the literature, particularly in the major review papers by Croze (1970) and Krebs (1973), in terms of the acquisition or reacquisition of a response to unfamiliar food stimuli. This view suggests that the bias should be a transient phenomenon, evident only during an initial phase of discovery and attribute learning. Once the food-related stimuli had been thoroughly learned, the

matching selection effect should diminish or disappear. We have shown, however, that there is a substantial perceptual bias even in selection among stimuli on which the animal has been overtrained, on a task at which it is performing at a maximum asymptotic rate, and similar steady-state results have been obtained in other naturalistic experiments (Dawkins, 1971b; Pietrewicz & Kamil, 1979). This implies the occurrence of major, reversible changes in the discriminability of a stimulus on a brief time scale, perhaps only a few milliseconds—changes that are suggestive of switching attention among target stimuli. The possibility that such attentional changes may play a major role in the search for cryptic food items has been mentioned several times in the literature, but the adaptive significance of the mechanism and the means by which it might produce matching selection have never been clearly articulated.

Attention to the features of a particular stimulus should tend to decrease the search time for that stimulus and increase the accuracy of its discrimination from the background. This increase in detectability is presumed to occur at the cost of overlooking other potential targets, however (Sutherland & Mackintosh, 1971). It is essential, therefore, that the animal not persist overlong in searching for a food type that is relatively uncommon or locally depleted. An attentional search for disparate, cryptic stimuli thus entails a decision procedure, that is, a means of determining how long to persist in searching for a given food type. The task is formally analogous to that faced by animals feeding on prey that occurs in disjunct aggregations or patches, who must determine when to relinquish searching in a given area and look for food elsewhere (Krebs, 1978). As in the case of patch-foraging, the allocation of searching effort among a set of alternative stimuli is most simply described in terms of a time threshold: The animal can be assumed to measure the elapsed time since the last item was detected and terminate its search when the time exceeds some predetermined threshold.

The “attention threshold” model of visual search for multiple targets thus involves an alternation of two modes: a slow, general search, in which the animal is receptive to the full spectrum of food stim-

uli, and a faster, more accurate specific search, in which it responds to one stimulus type exclusively (Figure 1). Discovery of a food item in the general mode is assumed to initiate specific searching for additional items of the same type. The animal persists in specific search until it encounters no additional food items for some threshold-time interval, whereupon it reverts to the general mode and begins broader sampling. The size of the threshold interval must be limited by the need to optimize the rate of food discovery. If the threshold chosen is too short, the animal will spend more time than necessary in the less effective general mode and will obtain less than its optimum rate of reward. If the threshold is too long, the animal risks persisting in a search for relatively uncommon grain types and overlooking more rewarding alternatives. Because the rate of discovery is a function both of food density and of conspicuousness, this argument suggests that the optimal threshold should be inversely proportional to the absolute density of food items and directly proportional to the degree of enhancement produced by switching from a general to a specific search mode.

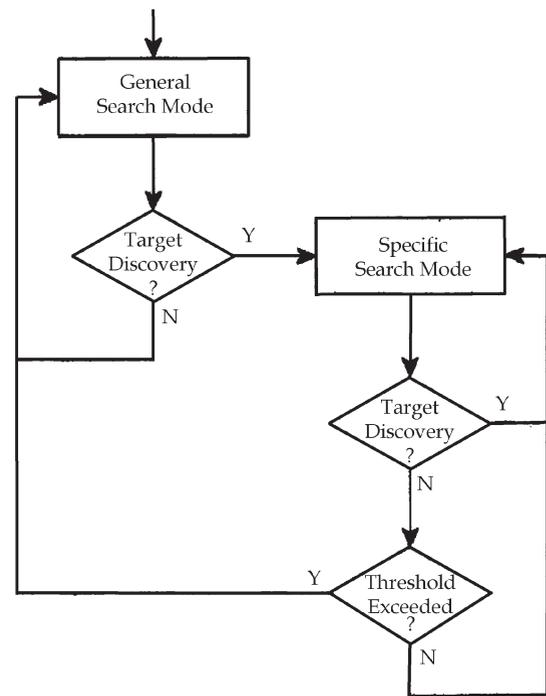


Figure 1. Flow diagram of the attention threshold model.

**Table 4.** Effects of Stimulus Type and Relative Proportion

Proportion (%) of beans	Majority grain type			
	Black gram		Wheat	
	Pecks /sec	Grains /peck	Pecks /sec	Grains /peck
100	2.56	.748	2.50	.648
90	2.40	.743	2.38	.670
80	2.40	.709	2.40	.642
70	2.35	.716	2.25	.645
(50)	(2.35)	(.678)		

Data in parentheses were not used in the analysis of variance.

One attractive feature of this model is that it offers a ready explanation for the influence of relative proportion on response rate. In the first experiment, the response rate was found to be significantly lower for samples containing equal numbers of the two grain types (Table 1). This effect was ascribed to response competition in the gray background treatments. In the mixed background, however, the response time contained a searching component, an additional delay that reflected the time required to discover the next food item. Because this suggests that the birds could seldom perceive more than one grain at a time, response competition seems to be a fairly unlikely source for the effect in the cryptic grain treatments. The attention threshold model, on the other hand, assumes that a lapse in attention during the search is inevitably followed by a transient decline in searching efficiency. This implies that a high rate of switching ought to yield a perceptible depression in the mean response rate. The probability of a lapse in attention between any two responses is minimized for samples containing only one grain type and maximized when the proportions are equal (see Equation A7 in the Appendix). By extension, then, the model predicts that the response rate should decrease significantly as the relative proportion of the two grains approaches equality.

With few additional assumptions, the attention threshold hypothesis proved to be amenable to an approximate analytical interpretation (derivation in the Appendix). Estimates of the model parameters could therefore be obtained by fitting the derived functional relationships to a set of experimental ob-

servations. Although the model is undoubtedly an oversimplification of the real-world process, its major features, particularly the inverse association between the generality and the speed of the search and the requirement that persistence in attending be attuned to short-term changes in the rate of discovery, appeared to be of sufficiently broad applicability to warrant a more detailed exploration of its consequences. An additional set of data was therefore obtained, which analyzed the animals' response to cryptic grain over a much wider range of relative proportions, and the results were reexpressed in terms of the model parameters.

## Experiment 2

### Method

This experiment employed the same subjects and procedures as the previous one, with the exception that only the most effective treatment combination, that of SS2 on a mixed background, was used. Each bird received three sessions of 10 trials each on nine relative proportions of the two grain types: 0%, 10%, 20%, 30%, 50%, 70%, 80%, 90%, and 100% black gram. To reduce the possibility of transfer between sessions of different types, all 30 trials with one subject and relative proportion were run on a single day in three blocks of 10 trials with roughly 1 hr.'s delay between blocks. The animal was then given 2 days of standardizing treatments, in which its daily grain ration was supplied in the experimental apparatus as a 50:50 mixture of SS2 on a mixed gravel background, followed on the third day by another set of experimental trials. Treatment order was fully randomized for each subject.

### Results

#### *Effects of Relative Proportion and Stimulus Type*

The treatments were classified according to the proportion of the majority grain (between 70% and 100%) and the majority grain type (black gram or wheat). The effects of these two variables on peck rate and accuracy were then determined with a two-way ANOVA (Proportion  $\times$  Majority Grain). Mean values for each treatment combination are displayed in Table 4.

There was a significant main effect of proportion on peck rate,  $F(3, 712) = 9.45$ ,  $p < .001$ , with a higher rate being exhibited on the more homogeneous sam-

ples. Peck rate was not affected by grain type, however,  $F(1, 712) = 2.39, p > .1$ , and there was no significant Proportion  $\times$  Grain Type interaction,  $F(1, 712) = .52, p > .6$ . In contrast, the only significant main effect for accuracy was with grain type,  $F(1, 712) = 38.2, p < .001$ . Accuracy appeared to be completely unaffected by relative proportion. It appears that the two grain types elicited relatively equivalent levels of responding but that pecks delivered to wheat were systematically less effective. All of these effects held true for each bird individually, as well.

#### *Analytical Model of Attention Threshold*

From the number of grains of each type presented and consumed in each trial, best-fit estimates of the attention threshold were obtained for each bird by a two-parameter, nonlinear least-squares fit to the selection curve (Equation A5). Threshold estimates are displayed for each bird in Table 5, and the fit of the computed functions to the raw data is shown in Figure 2. The fitted equations accounted for 94-95% of the variance.

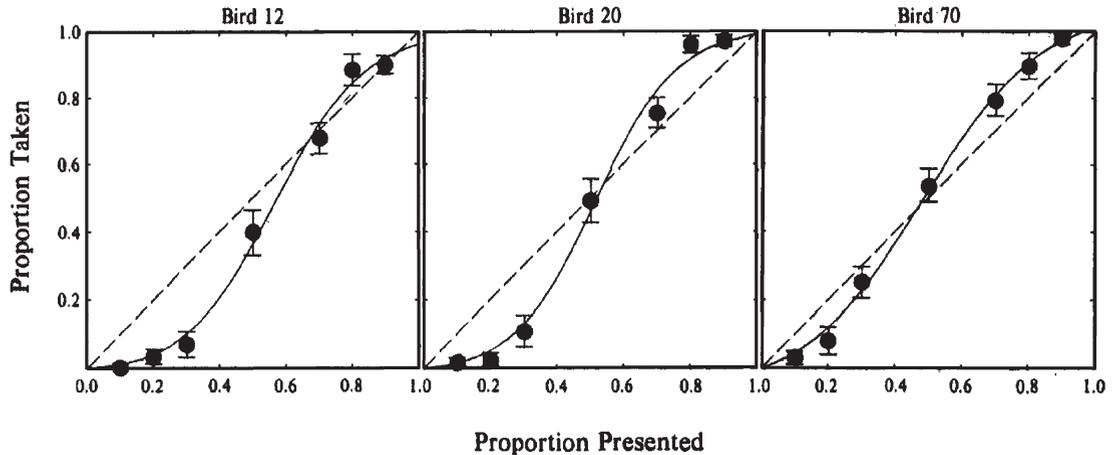
One measure of the increase in discriminability resulting from selective attention is the "searching coefficient," that is, the ratio of the search time per peck in the general mode to that in the specific mode. Using the information from the trial duration, the number of pecks, and the interpeck interval on the gray background (from Experiment 1), the search time per peck in the specific and general search modes was estimated for each bird by a two-parameter, nonlinear least-squares fit to the peck-time function (Equation A8). Estimates of the search time per peck and the interpeck interval for each attentional mode and for the search as a whole are given in Table 5, along with the estimated searching coefficient for each bird. The fit of the raw data to the peck-time function is displayed in Figure 3. The variance in the empirical data was fairly high, but the fitted equations still accounted for a significant proportion, especially in Birds 12 and 20, which had the lowest variance within treatments and the highest predicted curvilinearity: Bird 12,  $r(270) = .22, p < .001$ ; Bird 20,  $r(270) = .19, p < .002$ ; and Bird 70,  $r(270) = .10, p < .094$ .

**Table 5.** Measures Derived from Modeling Analysis

Measure	Bird		
	12	20	70
Time measures (in msec)			
Observed interpeck interval			
Mixed background	427	400	466
Gray background (from Experiment 1)	331	318	368
Specific search mode			
Search time per peck	51	46	47
Interpeck interval	382	364	415
General search mode			
Search time per peck	276	243	158
Interpeck interval	607	561	526
Threshold	116	109	52
Ratio measures			
Searching coefficient	5.43	5.24	3.34
Percentage of optimal performance	98.7	99.3	93.3

#### *Simulation Model of Attention Threshold*

To determine the degree to which the estimated threshold values maximized the rate of grain discovery, the behavior of each subject was simulated with a Monte Carlo model based on the algorithm in Figure 1. Twenty grains of two types, in predetermined relative proportions, were initially available for discovery. The program began in the general searching mode, in which the probability of discovery of a grain at any step was determined as a function of the number of grains of each type remaining. On discovery of a grain, the number of that type remaining was decremented. Grain discovery shifted the program from the general to the specific mode, multiplied the probability of discovery of the attended grain type by the searching coefficient, and reduced the probability of finding the unattended grain to zero. The program remained in the specific mode until a threshold number of successive unrewarded steps had been recorded, after which it reverted to the general mode. The trial was terminated when 10 grains had been discovered. The output variables from each trial consisted of the cumulative searching time in each of the two modes, as indicated by the total number of steps taken and the proportion of beans in the grain discovered.

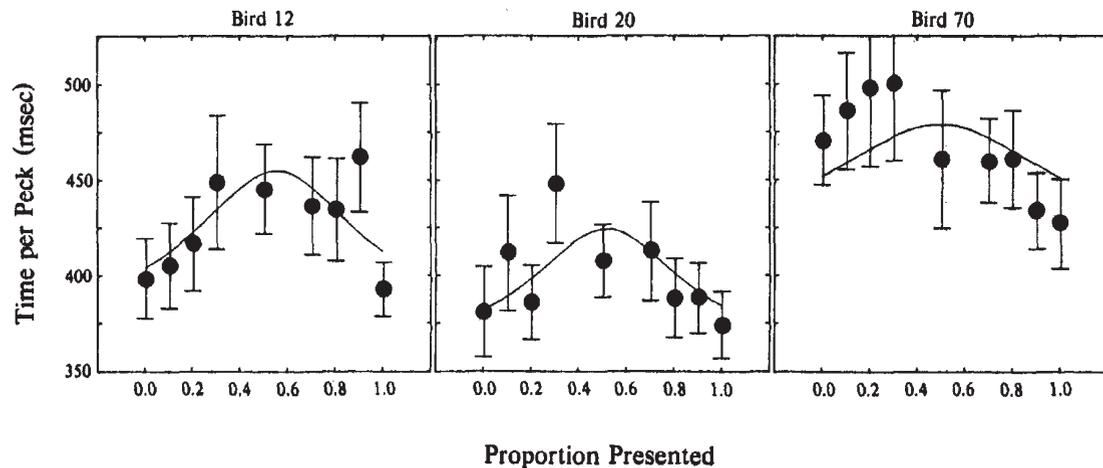


**Figure 2.** Selection curves for the three subjects. (Mean values for each treatment condition are plotted with filled circles. Hash marks indicate 2 SE. Solid line is least-squares fit of the raw data to Equation A5. The null hypothesis of indifference or lack of selection is shown with a dashed line.)

Using the estimated searching coefficient from each subject as input to the model, 200 trials were conducted at each of nine relative proportions (from .05 to .45) for simulation thresholds with 1 to 40 steps. Mean values of the searching time in each attentional mode and the proportion of beans taken were recorded for each combination of relative proportion and threshold. Curves describing cumulative searching time as a function of threshold were generated for each relative proportion for each bird and fitted by nonlinear least squares. Search time in the specific mode increased logarithmically

with threshold, whereas the search time in the general mode declined rapidly, approaching a stable asymptote. As a consequence, the total search time necessarily attained a minimum value at some optimizing threshold. The threshold associated with this minimum was calculated by setting the derivative of the function to zero and solving by iteration.

The optimum threshold was found to be greater than the empirical value for all birds by a factor of between 23% and 48%. The absolute deviation from optimal performance is not necessarily the best



**Figure 3.** Time per peck as a function of the proportion of black gram in the sample for each bird. (Means  $\pm$  2 SE are plotted for each treatment condition. The solid line represents the least-squares fit of the raw data to Equation A8.)

measure of searching efficiency, however. Because of the asymptotic decrease of general-mode search time with increasing threshold, the total search time decreases rapidly to a virtual plateau, increasing only gradually thereafter. Fairly substantial differences in threshold in the region of the optimum may, therefore, produce only a negligible effect on the duration of the search. The proportion of the optimum rate of discovery that the simulation model exhibited at the estimated empirical threshold for each bird is displayed in Table 5. This value was in all cases greater than 93%.

## Discussion

Matching selection was characteristic of the behavior of all three birds in this experiment (see Figure 2), though it was most evident for Birds 12 and 20. The analytical model attributed this bias to the influence of a switching threshold that, at first glance, seems remarkably brief—at most only twice the mean search time per peck in the specific mode. The estimated probabilities of a lapse of attention between successive responses were correspondingly higher than one might have expected, ranging up to .37 for a 50% mixture of the two grains. Intuitive feelings for the appropriate magnitude for these measures are unreliable, however. A lapse probability of even .4 is sufficient to produce a significantly nonrandom ordering in the sequence of grains removed. Over half of the runs in such a sequence will be longer than four items, whereas the comparable figure for a random ordering would be 13%.

The analytical model suggests that attention to the features of the target stimulus may decrease the search time per peck by as much as 80%. When switching delays and performance time are included, the model posits roughly a 25% increase in the rate of discovery over what would have obtained had the animal searched exclusively in the general mode. The response rate during selective search was remarkably uniform across subjects; most of the differences between subjects in the searching coefficient were attributable to differences in discriminative ability in the general mode. Zeigler (1976) observed minimal differences be-

tween subjects in peek time on conspicuous stimuli, but the possibility that attentional search in a more difficult task might exhibit a similar degree of invariance has not previously been proposed.

The suggestion that persistence in attending should be adjusted so as to optimize the rate of food discovery is consistent with the results of the simulation analysis. This is relatively weak evidence, however: The program demonstrated that the function relating cumulative search time and threshold has a broad and inapparent minimum and that substantial variations in threshold might have little detectable effect on the rate of discovery. More convincing indications of optimization can be found in the close correspondence between the estimates of threshold and searching coefficient across subjects. The similarity in the threshold estimates for Birds 12 and 20 is mirrored in their searching coefficients; the threshold for Bird 70 was conspicuously lower than that for the other two birds, and the searching coefficient was similarly reduced. Because the derivation of these measures in the analytical model entails no necessary dependence between them, the suggestion of some sort of compensatory interaction is almost unavoidable. Perhaps the simplest hypothesis is that subjects that find the discovery of a grain in the general mode more difficult tend to persist longer in attentional search for items of a similar appearance. This hypothesis appears to be testable in that it predicts a significant positive correlation between measures of attentional persistence and general-mode response time across a series of subjects on a range of different grains and backgrounds.

The central assumption of the attention threshold model concerns the existence of functionally distinct attentional states that differ in their characteristic rates of stimulus discovery. The assumption leads directly to the prediction that the mean peak rate should be maximized in samples consisting of a single grain type and minimized when the relative proportions approach equality. A simpler, alternative model of the allocation of attention, similar to models developed by Falmagne (1965) and Audley (1973) to describe choice reaction time, can be generated by assuming that the bird was always

attending to one stimulus or the other, but that the probability of being in a given attentional state was influenced by past experience. This fast-switching model eliminates the feature of the less efficient, general search mode and predicts no effect of relative proportion on response rate. To this degree, the dynamics of the threshold model appear to be supported: As in the first experiment, there was roughly a 10% difference in peck rate across the relative proportion treatments, a difference that was unaffected by majority grain type (Table 5).

Few other features of the model are open to test in an experiment of this kind, however. For example, the assumption of a constant switching threshold, independent of grain type and recent history of reward, is almost certainly unrealistic but cannot be disconfirmed in the absence of detailed information on the sequence and timing of individual responses. The assumption that attention to one stimulus is invariably associated with a decrement in the ability to discriminate the other has been asserted to be the critical feature that distinguishes attentional from associative models of discrimination learning (Mackintosh, 1975). It has been observed in studies of visual search in humans (Schneider & Shiffrin, 1977), though Blough (1979) found no evidence of such a decrement in pigeons searching for one or two target types in a uniform field of distractor elements. The results of the present experiment cannot speak to this issue, however. Because the maximum peck rate is presumably limited, any enhancement of responding to one stimulus type in a free-response design will necessarily be accompanied by a decrement in responding to the other, irrespective of changes in the absolute levels of discriminability.

What is most impressive in the results of this study is less the explanatory strength of any theoretical model than the levels of performance displayed by the animals. Pigeons are phenomenally good at this task. Any of the three subject birds could clear all 20 grains of even SS1 from a mixed gravel background in less than 15 sec, whereas even experienced human subjects (e.g., the experimenter) were seldom able to achieve the same result in under 2 min. Very little of this feeding time was taken up in searching. The mean interresponse interval in the

second experiment was about 430 msec, of which only perhaps 90 msec were apparently involved in the discovery of the grain. The fact that perceptual biases and time delays could still be demonstrated, even in the face of such expertise, suggests the operation of a robust and pervasive cognitive process, one that may well be characteristic of visual search for cryptic stimuli in other species.

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## Appendix

### Estimation of the Attention Threshold

We wish first to obtain an expression that predicts the proportion of Grain A (beans) in the diet,  $\hat{p}$ , given the proportion in the sample provided,  $p$ . If the intervening periods of general searching are ignored, the attention threshold model entails an alternation of two attentional states: State A, in which the bird is looking for or concentrating on Stimulus A, and State B. In State A, the bird finds only grains of Type A; in State B, it finds only grains of Type B. Each successive grain discovery thus provides an indication of the attentional state of the animal, and the sequence of items taken describes the output of a Markov process with the following matrix of transition probabilities:

		Subsequent state	
		A	B
Initial state	A	$1 - \alpha$	$\alpha$
	B	$\beta$	$1 - \beta$

If A grains and B grains are approximately equally conspicuous, the proportion of A in the diet will be equivalent to the proportion of time spent in State A. Over the long run, the latter will converge on the first stationary vector of the matrix, or

$$\hat{p} = \beta / (\alpha + \beta) \quad (\text{A1})$$

The central assumption of the attention threshold model is that the animal will switch away from its presently attended grain type when the elapsed time since the previous discovery exceeds a threshold value,  $\theta$ . Although feeding during the trial progressively depletes the available set of target grains, the fact that the trial is always terminated at about the same point in the depletion process allows us to approximate its dynamics with stationary equations and to treat the rate of grain discoveries as if it were a constant,  $r$ , equivalent to its average value. The search can then be approximated by a Poisson

renewal process, and the probability that an interval between successive discoveries will be longer than  $\theta$  can be expressed as  $e^{-pr\theta}$  in State A and  $e^{-(1-p)r\theta}$  in State B. These are the probabilities of a lapse in attention.

In order to switch from one attentional state to another, however, the bird must not merely lapse into the general mode but also must discover the opposite grain type immediately afterward. If the next encounter after the lapse is of the same type, the bird will simply resume attentional search and no switch will occur. The transition probabilities are, therefore, products of two event probabilities: (a)  $\alpha$  = the probability of lapse of attention in State A  $\times$  the probability that the next discovery is B, and (b)  $\beta$  = the probability of lapse of attention in State B  $\times$  the probability that the next discovery is A, or

$$\alpha = e^{-pr\theta} \cdot (1 - p) \quad (\text{A2})$$

$$\beta = e^{-(1-p)r\theta} \cdot p \quad (\text{A3})$$

Substituting Equations A2 and A3 into Equation A1 and setting  $k = r\theta$ , we obtain an expression for  $\hat{p}$ , the selection curve, in terms of  $p$  and  $k$ :

$$\hat{p} = \beta / (\alpha + \beta) = (e^{-(1-p)k} \cdot p) / [e^{-pk} \cdot (1 - p) + e^{-(1-p)k} \cdot p] \quad (\text{A4})$$

This equation is actually applicable only if the two stimulus types are equally conspicuous. Because this is seldom so in practice, an additional parameter, the bias factor,  $b$ , must be included. The residual variance in the experimental data was minimized by applying this bias factor to the discovery probability in the general mode:

$$\hat{p} = (e^{-(1-p)k} \cdot pb) / [e^{-pk} \cdot (1 - pb) + e^{-(1-p)k} \cdot pb] \quad (\text{A5})$$

Equation A5 enables us to estimate  $k$  and  $b$  through a least squares fit to the experimental data.

#### Derivation of the Searching Coefficient

Estimation of the searching coefficient requires an extension of the previous derivation to produce an expression for the probability of a lapse in attention in the interval between any two successive responses. This parameter, represented by  $\Phi$ , is simply  $\Phi$  = (Proportion of

time in State A  $\times$  Probability of lapse from State A) + (Proportion of time in State B  $\times$  Probability of lapse from State B), or,

$$\Phi = \hat{p} \cdot e^{-pk} + (1 - \hat{p}) \cdot e^{-(1-p)k} \quad (\text{A6})$$

Substituting for  $p$  from Equation A5 and canceling,

$$\Phi = e^{-k} / [e^{-pk} \cdot (1 - pb) + e^{-(1-p)k} \cdot pb] \quad (\text{A7})$$

If we postulate that a lapse of attention entails a uniform time penalty,  $C$ , which represents the mean additional time required to find the next grain in the general searching mode, the trial duration,  $T$ , can now be divided into two components, one attributable to specific search and one to general search. The former,  $T_s$ , is the product of  $t$ , the time per peck in the specific mode, and  $Z$ , the number of pecks in the trial. The general mode component,  $T_g$ , represents the time lost in switching away from an attentional search, so  $T_g = Z\Phi C$ . The total trial time can then be expressed as

$$T = T_s + T_g, \quad \text{or } T = Zt + Z\Phi C \\ = Z(t + \Phi C). \quad (\text{A8})$$

An estimate of  $\Phi$  can be obtained from Equation A7 and from the values of  $k$  and  $b$  derived previously. Using the empirical values of  $T$  and  $Z$  for each trial, best-fit estimates of  $t$  and  $C$  can then be obtained from Equation A8 by nonlinear least squares.

By factoring  $t$ , the time per peck in the specific searching mode, into a search phase of  $t_s$  and a movement phase of  $t_m$ , an estimate of the searching coefficient,  $a$ , can now be derived. The movement time per peck can be approximated by the peck time for homogeneous samples on a conspicuous background, which can be obtained by extrapolation from Experiment 1. The search time per peck in the specific mode is thus,  $t_s = t - t_m$ ; the search time per peck in the general mode is  $t_s + C$ . The searching coefficient is simply the ratio of these times:

$$a = (t_s + C) / t_s \quad (\text{A9})$$

An estimate of  $t$  also allows us to reexpress  $k$  as a true time threshold,  $\theta$ . Since  $k = r\theta$ , and  $r = 1/t$ ,  $\theta = kt$ .