

# THE 'PECK/NO-PECK DECISION-MAKER' IN THE BLACK-HEADED GULL CHICK

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The Choice Threshold Model (Dawkins 1969a, b) was proposed to account for the short-term determination of individual choice responses, such as pecks by chicks at coloured spots. Predictions (about strong stochastic transitivity, and cue additivity and cue opposition) have been tested and found reasonably successful. These predictions were concerned with percentage preferences, i.e. *relative* numbers of responses to different stimuli. This paper will deal with *absolute* numbers of responses, specifically pecks of the black-headed gull chick, *Larus ridibundus*. It should be emphasized that the ideas and conclusions presented here apply only to the present experimental situation, and have meaning only within the framework of the model. If the basic model is invalid, so are the present ideas.

Figure 1 explains the Choice Threshold Model in the terms with which it was previously introduced, of a fluctuating Variable V, interacting with thresholds corresponding to the stimuli. Preferred stimuli have low thresholds. During times when V exceeds the threshold of only one available stimulus, only that stimulus can be chosen. When no threshold is exceeded, no response can occur. When more than one threshold is exceeded, the corresponding stimuli are equally likely to be chosen.

This model is supposed to determine *which* of the available stimuli will be chosen whenever such a choice is to be made. It may be called the 'directing decision-maker'. It does not however determine *when* choices are made: that is supposed to be done by a separate 'go/no-go decision-maker'. This determines *sampling instants* (Fig. 1), at which the state of V relative to the thresholds is sampled, and a choice accordingly directed (or not if no threshold is exceeded). The frequency of such sampling instants or 'go decisions' will be represented by K. Thus the rate of responding to a singly presented stimulus

is given by the proportion of time V spends above the threshold of that stimulus, multiplied by K. When more than one stimulus is presented, the total rate of responding equals K times the proportion of time spent by V above the lowest threshold.

The value of K may fluctuate in time, but for the deduction of the predictions about percentage preferences already mentioned, it is necessary to assume that K is independent of the height of V. However there is no need to assume that it is independent of the stimuli presented. In this paper we shall investigate empirically the relationship between stimuli and K.

Consider an experiment in which three stimuli, say A, B and C, preferred in that order, are presented in all possible pair combinations, A with B, B with C, and A with C (Dawkins 1969a). Table I gives the numbers of responses expected to each stimulus in each situation, in terms of the proportions of time spent by V in various relationships to the thresholds, and in terms of K. Since we are investigating the possibility that K may differ with different stimulus situations, we must consider three Ks,  $K_{AB}$ ,  $K_{BC}$

**Table I. Numbers of Pecks Predicted by the Choice Threshold Model, at Three stimuli, A, B and C in Each of the Three Possible Pair Combinations**

Choice test	Number of pecks at stimulus		
	A	B	C
A with B	$K_{AB} \frac{(x+y+z)}{2}$	$K_{AB} \frac{(y+z)}{2}$	
B with C		$K_B \frac{(y+z)}{2}$	$K_{BC} \frac{(z)}{2}$
A with C	$K_{AC} \frac{(x+y+z)}{2}$		$K_{AC} \frac{(z)}{2}$

x, y and z are as in Fig. 1. Each expression is multiplied by the appropriate measure of the go/no-go decision-maker's activity,  $K_{AB}$ ,  $K_{BC}$ , and  $K_{AC}$  respectively for each of the three choice tests.

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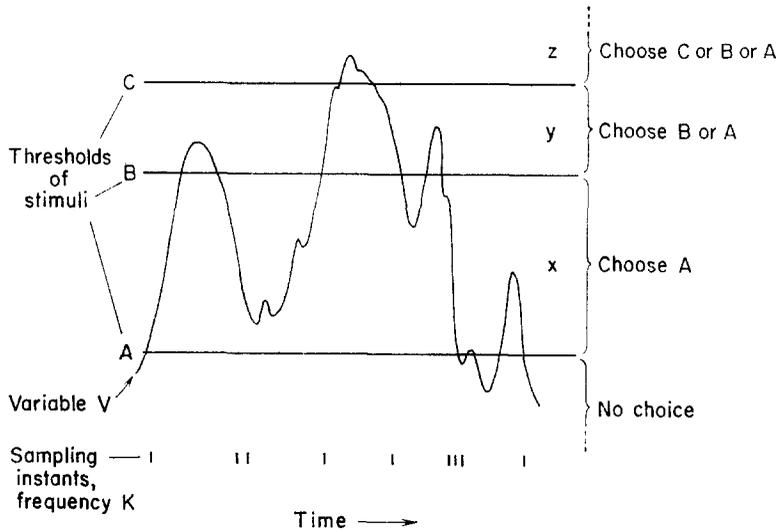


Fig. 1. The Choice Threshold Model. A hypothetical internal fluctuating variable,  $V$ , interacts with thresholds corresponding to external stimuli. Choices are made at specific *sampling instants* in time, determined by a separate *go/no-go decision-maker*, their frequency represented by  $K$ . A choice is equally likely to be directed at any stimulus whose threshold is exceeded by  $V$  at the *sampling instant*. Thus preferred stimuli are those with lower thresholds; here stimulus A is preferred to B which is preferred to C. The probability of  $V$  lying above A's threshold but below B's is  $x$ . The probability of  $V$  lying above B's (and therefore also A's) threshold but below C's is  $y$ . The probability of all three thresholds being exceeded is  $z$ . Therefore, e.g. if A is presented with B, C being absent, the number of choices of A will equal  $K(x + \frac{y+z}{2})$ , and the number of choices of B will equal  $K\frac{(y+z)}{2}$ . This is because during time  $x$ , all the choices will go to A, as the only stimulus whose threshold is exceeded, while during time  $y+z$ , both A's and B's thresholds are exceeded, and they must share the choices equally. In order for a choice to be made, it is necessary both that  $V$  should exceed at least one threshold of an available stimulus, and that the go/no-go decision-maker should order a sampling of the state of  $V$ .

and  $K_{AC}$ . Our question of the empirical data then becomes 'are these three  $K$ s the same as each other, and if not what relationship do they bear to each other?'

Let  $X$  [ $Y$ ] equal the number of responses to any stimulus  $X$  when it is presented together with  $Y$ . Thus  $A [B] + B [A]$  is the total number of responses given when A and B are presented together. Then from Table I:

$$A [B] + B [A] = K_{AB}(x + y + z)$$

$$A [C] + C [A] = K_{AC}(x + y + z)$$

Therefore 
$$\frac{A [C] + C [A]}{A [B] + B [A]} = \frac{K_{AC}}{K_{AB}}$$

Similarly it can easily be seen that

$$\frac{2 B [A]}{B [C] + C [B]} = \frac{K_{AB}}{K_{BC}}$$

and

$$\frac{C [A]}{C [B]} = \frac{K_{AC}}{K_{BC}}$$

By measuring these quantities therefore, ratios between the three  $K$ s can be estimated.

**Methods**

The experiments were originally done as part of a larger programme of research on colour preferences, using other responses as well as pecking, and with a different theoretical aim

(Impekoven 1969 will give further details of methods and results). The present theoretical treatment is an incidental by-product.

The subjects were chicks of the black-headed gull, *Larus ridibundus*, aged between 24 and 36 hr, who had been hand-fed. They were hatched in a darkened incubator, from pipped eggs taken from wild birds' nests at Ravenglass, Cumberland. After testing they were replaced in nests in the colony, where they seemed to be readily accepted by foster parents.

The normal feeding method of the young of this species is to peck at the bill of the parent, who then regurgitates food. It is known that long 'bill-shaped' objects are good stimuli for this pecking response, and colour preferences were therefore studied by giving the chicks choices between artificial 'bills' of different colours. Comparable studies are those of Tinbergen & Perdeck (1950), Weidmann & Weidmann (1958), Weidmann (1961), Franck (1966) and Hailman (1967).

For reasons not connected with the present topic, the initial approach response of the chick to the parent was of interest as well as the pecking at its bill: accordingly the different coloured 'bills' were presented attached to a life-size model of an adult gull, made of flat cardboard and painted light grey (Robbialac French grey, no. 435). Two 'bills' of different colours projected down below the 'head', one 'posterior' (on the model) to the other (Franck 1966). To increase the stimulating value, the whole model was moved from side to side, each complete movement cycle lasting about 1 sec, through a distance of about 2.5 cm. The background was of the same shade of grey as the gull model.

Six different colours were tested. Cardboard 'bills' were covered with papers from the Ostwald series, red (7 pa), yellow (2 pa), blue (13 pa), green (21 pa), black (grey p), and white (grey a). In a first series of experiments, involving 100 chicks, the six colours were presented equally often, in all 15 possible pair combinations, according to a Latin square design which eliminated position and order effects. Each individual chick received three choice tests, including all six colours. In a later series of experiments with 80 chicks, a similar Latin square design involving only eight pair-combinations was used, each chick accordingly receiving only two choice tests.

Each choice test lasted for 30 sec from the first peck, in which the number of pecks at each

of the two colours was counted. In the present paper, these results are mainly used in the form of mean numbers of pecks per min. In addition, a mean percentage preference (' $P_{sim}$ ') was

calculated for each pair of colours, as the mean of the individual percentage preferences as in Dawkins (1969 a and b). The individual percentage preference for each chick was the number of pecks at the normally preferred colour, divided by the total number of pecks at both. By 'normally preferred colours' is meant the colours which ranked higher for the average performance of the whole sample of chicks.

### Results

The order of preference was blue (B), red (R), yellow (Y), green (G), black (D), white (W) (cf. Weidmann & Weidmann 1958; Weidmann 1961; Franck 1966). A typical peck rate was 30 per min. Our formulae to estimate ratios between  $K_s$  referred to three stimuli, A, B and C presented in pairs, but the gulls were presented with six stimuli in all 15 possible pair combinations. It is possible to consider any three of these stimuli in order of preference as A, B and C. There are 20 such triplet combinations, each of which yields an estimate of ratios between the three  $K_s$ . For example the ratio  $K_{AC}/K_{AB}$  can be estimated as

$$\frac{R[G] + G[R]}{R[Y] + Y[R]} \text{ or as } \frac{Y[W] + W[Y]}{Y[G] + G[Y]}$$

or in any of 18 other ways. Mean ratios will be given, together with standard deviations, though the latter are probably not very reliable owing to the non-independence of the separate estimates.

The mean estimate of  $K_{AC}/K_{AB}$  is 0.991 (SD 0.063). This ratio is very close to 1, suggesting that  $K_{AB}$  equals  $K_{AC}$ . This conclusion is confirmed by the fact that the ratio  $K_{AB}/K_{BC}$  is found to be very similar to  $K_{AC}/K_{BC}$ . The means are respectively 0.696 (SD 0.169), and 0.685 (SD 0.221).

It seems then that  $K_{AB} = K_{AC}$  but  $K_{BC}$  is larger. In words this means that for any three stimuli, the activity of the go/no-go decision-maker when the first stimulus in order of preference is presented with the third, is the same as when the first and second are presented together, but it is higher when the second and third are presented together. This suggests a general

answer to the question raised above of whether the go/no-go decision-maker is controlled by the stimulus situation: it is, but only by the best available stimulus; other stimuli have no effect. Furthermore, perhaps a little paradoxically, inferior stimuli, when they do control the go/no-go decision-maker activate it more strongly than do superior stimuli when these are available.

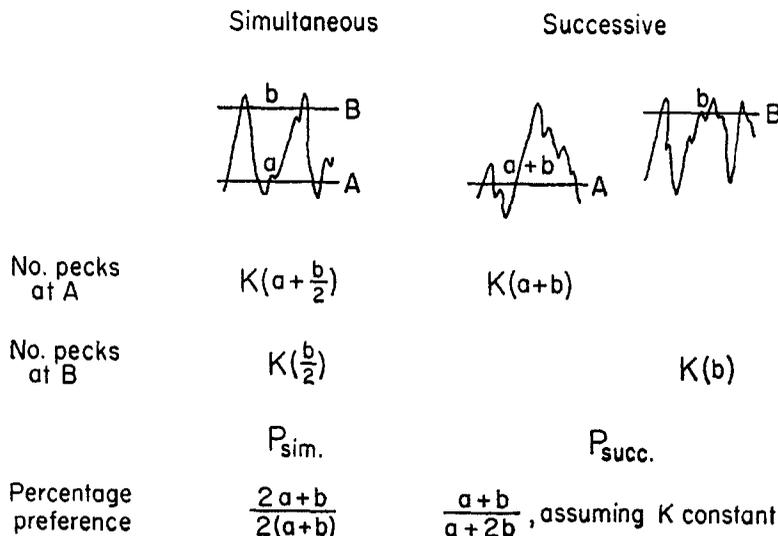
Thus there is a K specific to blue, which operates when blue is presented together with inferior stimuli such as red, yellow, and all the others of the present study. The K specific to red, which is higher, only operates when red is presented with stimuli inferior to it, yellow, green, black and white in the present experiments. The K specific to green, higher still in value, operates only when green is presented with black or white, and the K of black operates only in the choice test black with white. The K specific to white is not relevant in any of the present experiments, since white is never the best available stimulus.

These conclusions will be given quantitative expression later. Meanwhile we shall consider their consequences for a prediction of the model which may be of some practical interest.

### Simultaneous or Successive Presentation of Stimuli?

In many experimental studies of selective responsiveness, the stimuli to be compared have been presented *successively*, at different times, and the numbers of responses counted over a standard period. Other workers have presented their stimuli simultaneously in the form of a choice. Franck (1966) compared the two methods, in experiments on black-headed gull chicks, and found the simultaneous method much more sensitive for showing preferences.

For the present model to make a prediction about the relative merits of the two methods of presentation, it is necessary to make some assumption about K, the activity of the go/no-go decision-maker. The simplest assumption, that K remains constant, yields a precise prediction: if  $P_{sim}$  is the proportion of responses to the *preferred* stimulus when the two are presented together; and  $P_{succ}$  is the number of responses to the *preferred* stimulus when presented alone, divided by the sum of the successive responses to



$$\therefore \text{eliminating } a \text{ and } b, P_{succ.} = \frac{1}{3 - 2P_{sim.}}$$

Fig. 2. Threshold diagrams for 2 stimuli, A and B, presented simultaneously and successively, and deduction of prediction relating  $P_{succ}$  to  $P_{sim}$ : a is the probability that V will exceed A's threshold only. b is the probability that both thresholds will be exceeded.

both stimuli, the prediction is

$$P_{\text{succ}} = 1/(3-2P_{\text{sim}}).$$

The deduction of the prediction is given in Fig. 2. Qualitatively it means that  $P_{\text{sim}}$  should be larger than  $P_{\text{succ}}$ .

However as we have just seen,  $K$  is not always constant. We must modify the prediction accordingly.  $P_{\text{sim}}$  of course will remain the same, since  $K$  affects only absolute peck rate.  $P_{\text{succ}}$  however will be smaller than in Fig. 2, because the  $K$  which operates when the more preferred stimulus is presented will be smaller than the corresponding  $K$  for the less preferred stimulus. Our modified prediction therefore is that  $P_{\text{succ}}$  should be even smaller in relation to  $P_{\text{sim}}$  than the formula above suggests. Franck's (1966) results confirm this.

We have not done any successive presentation tests as such. However it is possible to use our data in an indirect way to test the expectations of the model. When young birds are presented with different coloured stimuli to peck at, there is always a possibility that they may direct some pecks to other objects in the situation, smears of dirt, or corners of the testing box perhaps. Both in successive and simultaneous presentation tests these are ignored as constant features of the background. In the same way, there is no reason why we should not regard deliberately presented stimuli as part of the background, provided they are constantly present. Thus for example the number of pecks at blue when it is presented with white, and the number of pecks at red when it is presented with white can be used to measure the successive presentation preference for blue over red; the numbers of pecks at white in the two cases are simply ignored.

The present hypothesis however requires us to take these background stimuli into consideration insofar as they affect  $K$ . If the constant background stimulus is superior to both the successively presented test stimuli,  $K$  should be constant in the two tests since it is determined by the best available stimulus. Therefore under these circumstances the formula given above should accurately predict the relationship between  $P_{\text{succ}}$  and  $P_{\text{sim}}$ . If the constant background stimulus is inferior to both test stimuli

however, the relationship between  $P_{\text{succ}}$  and  $P_{\text{sim}}$  should be the same as if there were no 'background stimulus':  $K$  will be determined by the successive test stimuli, and as argued above,  $P_{\text{succ}}$  will be even lower in relation to

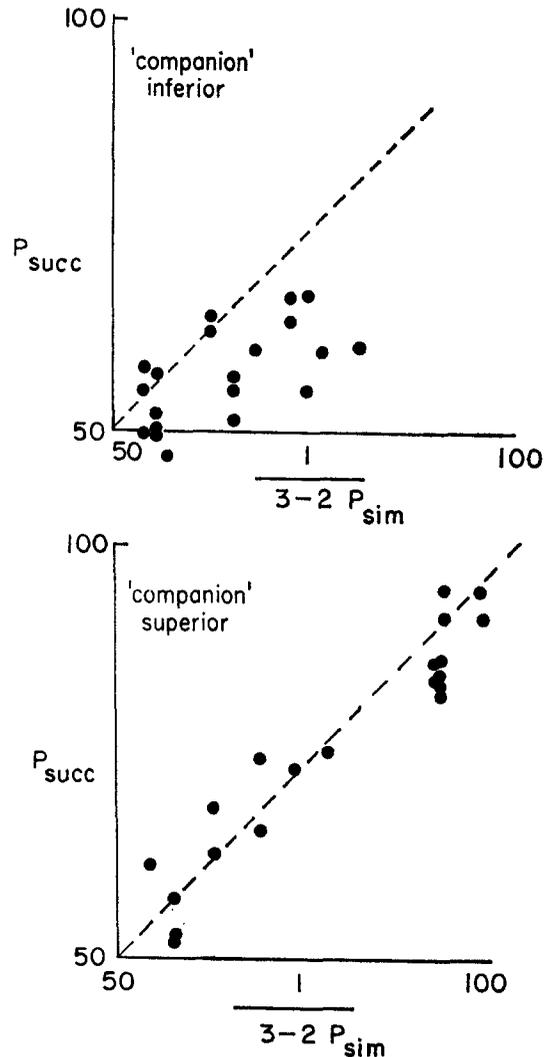


Fig. 3. Indirect test of simultaneous/successive prediction. Both graphs are scatter diagrams of observed  $P_{\text{succ}}$  against that predicted by  $P_{\text{succ}} = 1/(3-2P_{\text{sim}})$ . The upper graph is for the cases where the 'background' or 'companion' stimulus (see text) was inferior to both test stimuli. The lower graph is for the cases where the 'background' stimulus was superior to both test stimuli. In the light of the findings about the relationship between  $K$  and the stimulus situation, a good fit (points lying close to 45-degree line) is expected in the lower graph, but not in the upper one.

\*Dr U. Weidmann (pers. comm.) has shown that this prediction adds nothing new if it is already known that Prediction 1 (Dawkins, 1969a) is true.

$P_{sim}$  than the formula predicts. Fig. 3 shows that both of these two expectations are borne out by the data.

### Measuring Threshold Values and Ks

We have reached the qualitative conclusion that  $K$ , the activity of the go/no-go decision-maker, is determined by the most preferred stimulus available. Let  $K_B$  be the  $K$  which operates when blue is the best stimulus presented, and let  $K_R$ ,  $K_Y$ ,  $K_G$ ,  $K_D$ , and  $K_W$  respectively be the  $K$ s specific to red, yellow, green, black and white.

The relative values of the different  $K$ s can be calculated from the data; first it is necessary to work out the *threshold* values ( $\theta$ ) of the colours, using the rules of the model summarized in Fig. 1. The threshold value  $\theta$  of a stimulus is a measure of the time spent by Variable  $V$  above its threshold. Thus a preferred stimulus, having a low threshold, has a large  $\theta$ . From Fig. 4

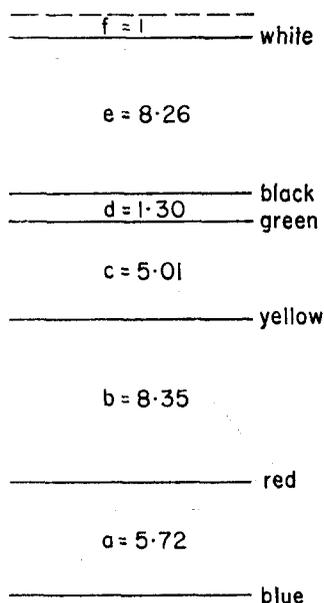


Fig. 4. Threshold scale diagram for the six colours. The symbols, and their calculated values between the lines represent *inter-threshold values*. That is, they are proportional to the time spent by  $V$  between the thresholds concerned. The distance between the lines is proportional to the corresponding inter-threshold value. The *threshold value*  $\theta$  of each colour is a measure of the amount of time spent by  $V$  above its threshold. It is represented by the distance of the appropriate threshold line from the dotted line at the top.

$f$  is the  $\theta$  of white,  $e + f$  that of black,  $a + b + c + d + e + f$  that of blue.

Numerical values of these inter-threshold values given in the figure were calculated as follows.

We arbitrarily let  $f$ , the threshold-value of white, equal 1. Then, following the rules of the model, given in Fig. 1,  $e$ , the inter-threshold value between black and white, can be obtained from the observed mean percentage preference ( $P_{sim}$ ) for black over white,  $P_{DW}$ , by solving the equation

$$P_{DW} = \frac{2e + f}{2(e + f)}$$

The mean percentage preference in this case was found empirically to be 94.6, and  $e$  is therefore 8.26. The threshold value,  $e + f$  of black, is therefore 9.26.

The value of  $e$  so obtained may be used to obtain two values of  $d$ , the inter-threshold value between green and black, from the equations  $P_{GD} = \frac{2d + e + f}{2(d + e + f)}$  and  $P_{GW} = \frac{2(d + e) + f}{2(d + e + f)}$ , where  $P_{GD}$  and  $P_{GW}$  are respectively the mean percentage preference for green over black, and that for green over white. The mean of the two values of  $d$ , together with  $e$  and  $f$ , is then used in the same kind of way to calculate three values of  $c$ . Four values of  $b$ , and five of  $a$ , are then obtained by the same method, and the mean is taken in each case.

Figure 4 is a scale diagram (cf. Guilford 1954) for the six colours: the distances between the lines are proportional to the mean inter-threshold values, i.e. to the time spent by Variable  $V$  between them.

The mean inter-threshold values can then be used to calculate values of  $K$  for each colour, using in this case the absolute numbers of pecks observed. Thus  $K_D$ , the  $K$  which operates when black is the best available stimulus, can be obtained by solving the equation  $D[W] = K_D(e + f/2)$ , where  $D[W]$ , it will be remembered, is the mean number of pecks at black when it is paired with white. Since white is an inferior stimulus to black,  $W[D]$ , the number of pecks at white when paired with black, is influenced by  $K_D$ , not  $K_W$ . Therefore, another value of  $K_D$  can be obtained from the equation

$W[D] = K_D (f/2)$ . Similarly four values of  $K_G$  can be calculated, two from each of the two choice tests in which green is the preferred stimulus. Six values of  $K_Y$ , eight of  $K_R$  and ten of  $K_B$  are all worked out in the same way.  $K_W$  cannot be obtained by this method, as white is never the best available stimulus. There is encouragingly little variation in the different values of  $K$  for each colour (Table II). The mean  $K$  for each colour will be used below.

Table II. Calculated Values of  $K$  for Each Colour when Presented with Each Inferior Colour

	$K_B$	$K_R$	$K_Y$	$K_G$	$K_D$
Paired with					
R	1.20				
R	1.16				
Y	1.20	1.24			
Y	1.12	1.90			
G	1.16	1.56	2.08		
G	0.98	1.32	1.60		
D	1.16	1.50	2.20	2.48	
D	1.00	1.12	1.68	2.00	
W	1.18	1.36	2.14	1.84	2.46
W	1.72	1.68	3.20	4.16	3.36
Mean	1.18	1.46	2.14	2.62	2.92

Unit of measurement:  $K$  here is that number by which the corresponding  $\theta$  must be multiplied in order to obtain the total number of pecks per min.

We are now in a position to see if there is any lawful relationship between the threshold value  $\theta$  of a colour, and its  $K$ , by plotting, for each colour, these two values against each other (Fig. 5). The relationship is *inverse*, and the points fall on a smooth curve (the actual curved line drawn in Fig. 5 is explained in the Discussion).

Since both threshold values and  $K$ s have been calculated ultimately from the same data, the suspicion may arise that a smooth inverse relationship of this kind is an inevitable artifact of the method of calculation. However this is not the case: testing with nonsense figures shows that any relationship between  $\theta$  and  $K$ , lawful or chaotic, positive or negative, is in

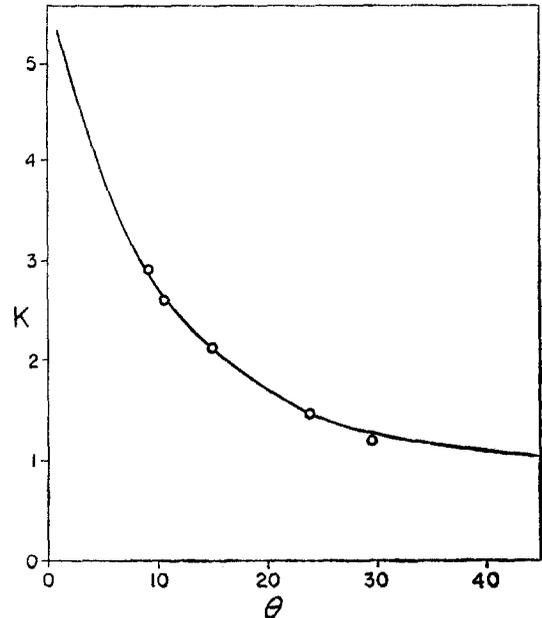


Fig. 5. Graph of  $K$  against  $\theta$  for five colours.  $K$  is proportional to the number of 'go decisions' of the 'go/no-go decision-maker' per minute.  $\theta$  is proportional to the time spent by  $V$  above the threshold of the colour concerned. The open circles represent the results calculated from the gull data. The solid line drawn in was generated by a computer model explained in the Discussion.

principle possible. The smooth relationship shown in Fig. 5 is a real property of the chicks.

### Discussion

The Choice Threshold Model has proved quite successful in accounting for percentage preference data—*relative* numbers of responses given to stimuli in simultaneous choice tests (Dawkins 1969a and b). The present paper has shown that *absolute* rates of responding cannot be accounted for by this model alone, and a separate go/no-go decision-making mechanism must be postulated.

The external stimuli which are pecked by black-headed gull chicks influence pecking in two different ways, a dichotomy reminiscent of that between 'releasing' and 'directing' in classical ethology (Tinbergen 1951; Franck 1966). Firstly ('directing' function), by fixing 'thresholds', stimuli influence the *relative* probability of their being pecked rather than other stimuli presented at the same time; thus blue is more likely to be pecked than green in a choice test. Secondly ('releasing' function) stimuli influence the go/no-go decision-maker and thereby have a non-discriminatory effect on the *absolute* rate of pecking at all available stimuli.

The first of these two influences is the determinant of percentage preferences in simultaneous choice tests, and it may have a limiting effect on absolute response numbers. The second influence affects absolute response numbers, but has nothing to do with percentage preferences in choice tests.

Out of any set of simultaneously available stimuli, only one, the most preferred, affects the go/no-go decision-maker. A somewhat paradoxical finding is that stimuli which have a high *relative* probability of being pecked tend to have low power to activate the go/no-go decision-maker and vice versa. These findings suggest a post-hoc model of the go/no-go decision-maker.

Suppose that the probability of a 'go' decision from the go/no-go decision-maker builds up like water in a cistern (Lorenz 1950) during time intervals when no pecks occur, and is abruptly reduced after a peck. It would thus tend to build up to higher levels during times when  $V$  was below all thresholds and no pecks could occur. The finding that  $K$  is determined solely by the best available stimulus is therefore explained, since  $V$ 's failure to exceed any threshold is of course synonymous with its failure to exceed the lowest threshold, i.e. that of the most preferred stimulus. The model also explains the paradoxical *inverse* nature of the relationship between  $\theta$  and  $K$ ; when a strong (i.e. low threshold) stimulus is available, relatively little time will be spent by  $V$  below all thresholds, and therefore relatively little time would be available for the build-up of 'go' probability.

A ('Monte-Carlo') computer simulation of this model was programmed. Various detailed versions of the model were tried. For example the build-up of 'go' probability over time was represented as exponential (like a capacitor charging up) or as linear (like a water tank filling up), and many values of parameters were tried. Various simplifying assumptions were made, for example the time taken to give a peck was regarded as negligible, and periods of total non-concern with pecking (e.g. preening or sleeping periods) were not considered.

All versions of the model yielded an inverse relationship between  $K$  and  $\theta$ , and in all cases the curve was shaped like that from the gull data, though it did not in all cases accurately match it in slope. The version of the model which gave the most precise fit to the observed data was the following:

Build-up of 'go' probability: shallow linear

(increasing by 0.025 every 0.107 sec since the last peck) up to 1, then flat (cf. cistern full to brim). Reduction of 'go' probability after 1 peck: steep linear (decreasing by 0.5 after each peck) down to 0, then flat (cf. cistern empty). The curved line drawn in Fig. 5 was generated by many runs of this particular version of the model. Doubtless an even better fit to the observed data could be achieved by further manipulation of parameters.

However, there seems little value in pursuing post-hoc contrivance further, when only gross rate measures of behaviour are available. The next stage should be to analyse the actual patterning of pecking in time (Blough 1963). This might eventually lead to the total abandonment of the theoretical ideas put forward in these papers, but their comparative success in matching behavioural facts measured at the cruder level, gives some reason to hope that they may profitably be used as a base on which to build models commensurate with a deeper level of practical analysis.

#### Summary

1. In companion papers a model called the Choice Threshold Model was described, and its applicability to percentage preference data tested. The present paper extends the treatment to absolute numbers of responses in a choice situation.

2. It is postulated that while the Choice Threshold Model functions as a 'directing' decision-maker, determining how choices are to be directed, the determination of when and how often such choices shall occur may be the function of a separate 'go/no-go decision-making mechanism', the rate of whose activity is represented by the symbol  $K$ .

3. Data on rates of pecking at coloured stimuli by black-headed gull chicks *Larus ridibundus*, are used to determine the relationship between  $K$  and the stimulus situation.

4. It is found that  $K$  is determined only by the most preferred stimulus available.

5. Thus a stimulus affects the animal in two different ways. By influencing the 'directing decision-maker' (the Choice Threshold Model), it affects the *relative* number of times it is chosen compared with other simultaneously available stimuli. By influencing the 'go/no-go decision-maker', which it only does when it is the most preferred of the available stimuli, it affects the *absolute* rate of choosing regardless of which stimulus is chosen. This dichotomy is reminiscent

of that of classical ethology between 'directing' and 'releasing' roles of stimuli.

6. Paradoxically it is found that stimuli which are preferred with respect to their 'directing' function tend to have low 'releasing' value and vice versa.

7. A quantitatively precise prediction concerning the relative merits of two methods of studying selective responsiveness, simultaneous or successive presentation of stimuli, can be derived from the model if it is assumed that  $K$  is constant. In the light of the findings about the dependence of  $K$  on the stimulus situation, this prediction has to be modified. The present data are used in an indirect way to verify the modified prediction.

8. The actual values of  $K$  (i.e. 'releasing' value) for each colour are estimated from the data, and are plotted graphically against the corresponding threshold values (i.e. 'directing' value). The inverse relationship appears to be a regular one, for the points all fall on a smooth curve.

9. These findings can all be explained by a Lorenzian hydraulic type of model. Various versions of the model have been simulated, and the parameters of one version adjusted to achieve a precise fit to the gull data.

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#### ERRATA

R. Dawkins (1969). A threshold model of choice behaviour. *Animal Behaviour*, **17**, 1.

p. 128, Fig. 4 — a point (coordinates 68·6, 88·2) has been omitted in the top left-hand graph.

p. 128, col. 1, line 4 — ' $P < 0·05$ ', should read ' $P > 0·05$ '.