A PROBABILISTIC MODEL OF THE SPATIAL PATTERNING OF PECKING IN BIRDS : PILOT
STUDY WITH YOUNG CHICKS.

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ABSTRACT

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ning of pecking in birds : pilot study with young chicks. Behav. Processes,
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     The pecking behaviour of young chicks (Gallus gallus) is studied in a
situation involving several equivalent targets (mealworms). The question is
raised whether the successive pecks are randomly distributed or whether they
follow a systematic order based on the spatial arrangement of the targets.
Data collected with one-week-old chicks indicate that pecking is compatible
with a probabilistic model where the probability to peck at a given place is
inversely proportional to the energy used for this particular peck. Pecking
by chicks is interpreted as a functional compromise between random sampling
and optimal exploitation of the environment.

INTRODUCTION

     The pecking activities of chicks have been the subject of a large number

of studies : these have dealt with food stimulation particularly from the

points of view of perception (Fantz, 1957 ; Dawkins, 1968 ; Goodwin and Hess,

1969 ; Dawkins, 1971 ; Willis et al., 1980) and motivation (Hogan, 1971).

     Other investigations have focused on the development of pecking accura-

cy (Cruze, 1935 ; Vauclair and Bateson, 1975) and on the temporal patterning

of pecking (Machlis, 1977).

     The aim of the present study is to examine an aspect of chick's pecking

that does not seem to have received much attention so far, i.e. the spatial

patterning of pecking involving no locomotion. We have investigated the ac-

tual intake of food from a set of food items lined up on the ground along

the bird's frontal plane. Spatial patterning was thus studied in a single

dimension - the lateral movements of the beak at it takes hold of the food

and swallows it - with a view to detecting any underlying one-dimensional

patterns (such as sequences, alternations, etc.).

     The particular characteristics of the experiment were that :

1) edible targets were used ;

2) targets were identical ;

3) locomotion was prevented.

Our investigations were aimed at detecting any regularities inherent to this situation. We nevertheless work on the assumption that any such regular patterns underlie a mode of behaviour that is of an essentially probabilistic nature : this study is part of a wider research topic centering on the claim that behavioural variability is valuable from an adaptative biological point of view (Bovet, 1979, 1983).

For this reason, the data provided by this experiment will be analysed in relation to the predictions of a probabilistic rather than a deterministic model. Both the data analysis and the model will involve some partial characteristics (location of the first targets to be pecked, the types of pecking sequences noted at the beginning of feeding) as well as one overall characteristic (the number of sequences per trial) of the pecking patterns.

METHODS

Subjects

Four domestic chicks (Gallus gallus) from a commercial hatchery were used. The subjects were kept together in a large cage where they were fed with a mixture of grains. The chicks were 6 to 8 days old.

Apparatus

The experimental set-up consisted of an opaque box (7 x 10 x 12 cm) in which the chick was placed. One side (7 x 12 cm) was provided with an opening allowing protrusion of the bird's head only ; between trials, this aperture was closed with a shutter.

The food "targets" consisted of mealworms cut up into similar 2 mm lengths. At each trial, 10 targets were lined up 1 cm apart on a white horizontal surface ; the row of targets was parallel to the box aperture and 1.3 cm away from it ; targets were numbered from 1 to 10 and the centre of the box aperture was located between targets 5 and 6 (Figure 1).

Lighting in the room in which the experiment took place was constant.

Procedure

Each of the birds underwent 4 sessions in the space of two days, at the rate of 2 sessions a day. On average, each session consisted of 7 trials, but the number of trials carried out at each session (see Table I) depended on how soon the animal's hunger was satisfied. A trial consisted of the eating of all 10 targets in succession. Between trials, a break of around 30 seconds occurred, during which a fresh row of targets was set up.
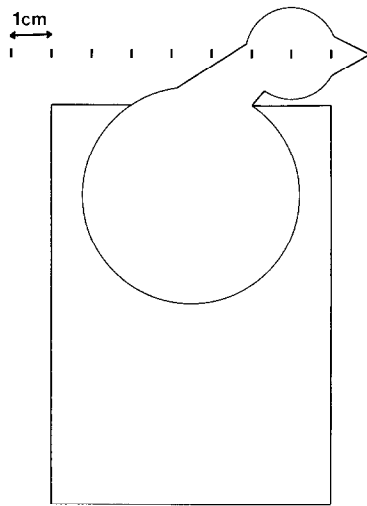
Fig. 1. Scale drawing of the experimental set-up.

RESULTS

Those main aspects of our results likely to come under scrutiny in re-
lation to our model predictions are presented below. In presenting these re-
sults, the data collected for the various individual subjects have been poo-
led in order to obtain sufficient numbers for statistical interpretation.
Individual results are nevertheless listed in the tables.

bird	session				mean
	1	2	3	4	
1	6.67 (3)	5.00 (9)	4.20 (10)	5.30 (10)	5.00 (32)
2	7.50 (2)	7.25 (4)	5.17 (6)	6.25 (4)	6.25 (16)
3	4.80 (5)	4.38 (8)	5.14 (7)	4.80 (5)	4.76 (25)
4	5.50 (10)	5.00 (10)	4.56 (9)	4.17 (12)	4.78 (41)
m	5.70 (20)	5.13 (31)	4.69 (32)	4.90 (31)	5.04 (114)

Table I. Mean number of sequences par trial (and number of trials).

Distribution of the first targets to be pecked

In our experimental situation, the most favourable moment for investigating the spatial patterning of pecking is at the beginning of each trial, when the chick has not yet modified the environment by its pecking. Figure 2a (full lines) therefore shows the distribution of the first targets to be pecked in each trial (total number of trials : 114). It was observed that the various target locations were far from eliciting an equivalent degree of preference (p (x_9^2 = 116.88) < 10^{-4}) : the first pecks showed a preference for targets 5 and 6, situated in the middle of the row. Good symmetry can moreover be noted in choice frequencies with respect to this mid-point. This result is in agreement with observations of the variability of pecking in the field of operant conditioning (Eckerman and Lanson, 1969).
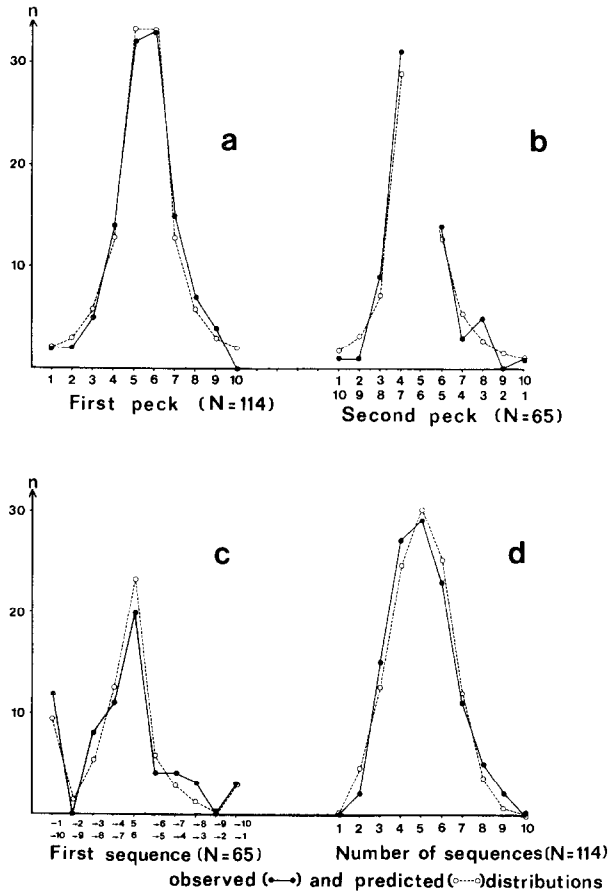

Fig. 2. Summary of group data and model predictions (see also Table II).

Distribution of the second targets to be pecked

A valid comparison of second pecks can only be made on the basis of situation that are identical, or at least analogous. This is why our study of second pecks was restricted to those cases where the first peck was aimed at a central target (n° 5 or 6) : these two targets being symmetrical, they were taken together. It can be seen that this analysis thus deals with 57 % of the previous trials (total number of trials : 65). Figure 2b (full lines) shows the distribution of second pecks subsequent to a central initial peck.

Here again, the various remaining target locations are far from being equivalent (p (χ^2_8 = 124.65) < 10^{-4}). Two of the effects observed with first pecks are seen to recur : a preference for any remaining central food items, and a more or less regular decrease of choice frequencies as the distance from the first peck increases. Unlike the first peck, however, a very clear distribution asymmetry is noted here : if the first peck is considered to divide the remaining targets into two groups forming a "smaller" and a "larger" region, it can be seen that at the second peck, the targets belonging to the "smaller" region are on the whole chosen more often than the targets belonging to the "larger" region (p (χ^2_1 = 5.55) < .025). We shall show that our model gives an interpretation of this effect involving the direction taken by the bird's head at the first peck.

Distribution of first sequences

The distribution of second pecks shows a high frequency of pecks aimed at adjacent targets. This is why, within the limits of the 65 trials which began with a central peck, we shall now deal systematically with series of successive pecks directed towards adjacent targets. We have called these series sequences.

Figure 3 presents the data from Figure 2b from a different angle, in the form of the overall distribution of all sequences beginning with a central peck, including those sequences that are composed of a single peck only (shaded columns).

Figure 3 calls for three comments. First, there is a marked symmetry between sequences beginning with target 5 (upper part of the Figure), and those beginning with target 6 (lower part of the Figure) : these sequences are almost identical in number, as we saw when analysing the first pecks, and have a very similar distribution in terms of their orientation (towards the "smaller" or the "larger" region) and their length (the number of contiguous pecks).
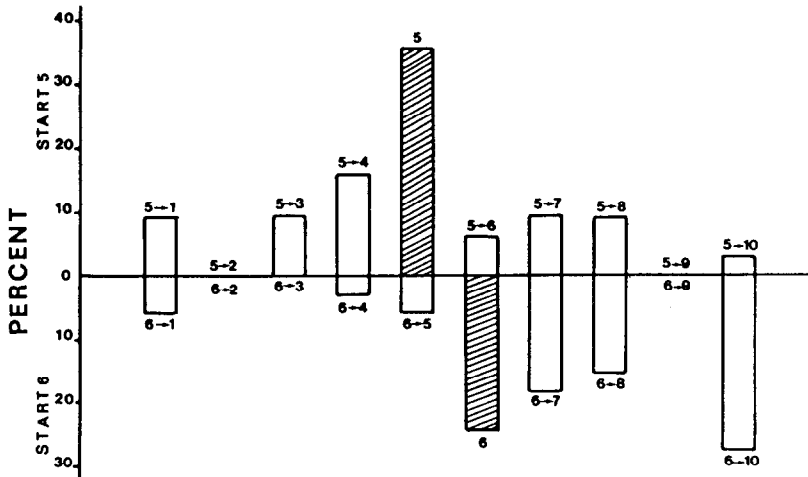
Fig. 3. First sequence of pecks. Arrow indicates adjacent pecks.
E.g. 5 → 1 means that the targets 5, 4, 3, 2, 1 are taken in that
order. See text for further explanation. (N = 114).

With regard to the orientation, if we take into consideration only se-
quences containing at least 2 pecks, we notice a very considerable differen-
ce (p (χ^2_1 = 6.42) < .025), the smaller zone having much higher numbers.

Lastly, an effect concerning the length of sequences is worth mentio-
ning : for lengths of sequences from 1 to 4, a regular decrease in numbers
is observed as the length of each sequence increases ; whereas for all se-
quences (length 5) culminating in the pecking of an item at the end of the
row, a sudden rise in numbers is observed. It is striking, in fact, that no
sequence ever occurs in such a way that an end-of-row item is left over
(which would be the case if sequences culminated at targets 2 or 9).

The above effect may be interpreted as indicating strategic behaviour
intended to reduce the overall amount of head movement required during a
trial. It will be seen that our model provides a very simple explanation for
this phenomenon.

Distribution of the number of sequences per trial

The study of first sequences presented above suggests that the organi-
zation of pecking into sequences is a characteristic that is likely to ac-
count for the organization of pecking in the situation under study.

The notion of sequence such as we have defined it (a series of contiguous pecks) enables us moreover to characterize the overall pattern for a whole trial : each pattern presents a number of distinct sequences ranging in number from 1 to 10.

Figure 4 shows a typical example of a pecking pattern, consisting of 4 sequences of lengths 5, 1, 2 and 2.
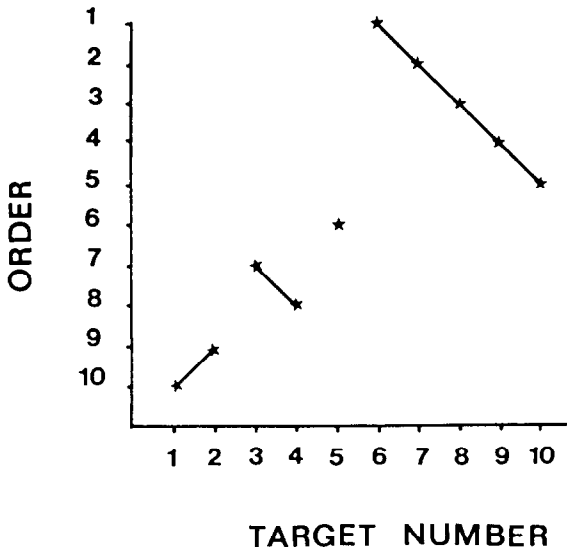

TARGET NUMBER

Fig.4. Pecking of 10 aligned targets. Example of one trial. Adjacent pecks are joined together to show up the sequences.

It is thus possible to establish the number of sequences per trial for the data taken as a whole (total number of trials : 114). Figure 5 presents this distribution along with the theoretical distribution that would result from absolutely random pecking.

These distributions are seen to be very distinct (p $(\chi^2_4 = 873.36) < 10^{-4}$): the patterns observed show a much "smaller" number of sequences than random patterns. Since the sum of the sequence lengths within a trial is constant, this amounts to making the following statement : the sequences observed are significantly "longer" than would be produced by pecking that is purely the result of chance, i.e. pecking where the remaining targets all have the same likelihood of being chosen at all times.
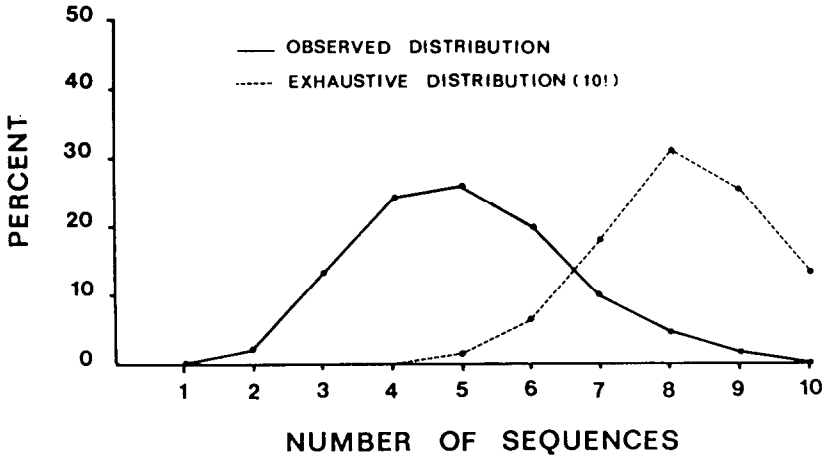
Fig. 5. Sequences in pecking of the 10 targets. Comparison of observed data
with a purely random model.

It will be seen below that a relatively simple modulation of this pro-
bability makes it possible for our model here again to predict theoretical
expectations in keeping with the observed data.

Changes in the number of sequences per trial, for each session and each
subject

The number of sequences composing a trial provides us with a simple in-
dex with a regular overall distribution (cf. Figure 5), that may show up pos-
sible variations in pecking mode between subjects and from one session to
another.

Table I presents the mean number of sequences per trial per subject and
per session.

Variance analysis (VAR 3 program, Rouanet and Lépine, 1977) shows the
following effects : there are significant differences from one session to
another (p < .025), this effect taking the form of a linear decrease in the
number of sequences, and the performances differed from one subject to ano-
ther (p < .001), but the session linearity x subjects interaction is not si-
gnificant.

These results therefore point to a degree of heterogeneity in pecking
patterns among subjects. They show in particular that the majority of the
animals adapted to the situation to some extent from one session to another

by changing their pecking patterns. We shall not, however, attempt to account
for these differences between subjects and between sessions in our model. We
are unable to fit the model parameters to the partial data in this study be-
cause of the small numbers available.

THE MODEL

We propose to account for most of the results mentioned above, using a
probabilistic model. It will thus be attempted to explain the main aspects of
pecking in this situation with reference to the simplest possible mechanisms.

For reasons of statistical power, this model will be adjusted and compa-
red to overall data established for the group of subjects as a whole. It is
nevertheless capable, by reason of its basic principles, of accounting for
individual data.

Our model is based on the following principles :
a) the target chosen at each peck is selected probabilistically from among
all the remaining targets ;
b) the probability of a target's being chosen is a decreasing function of its
distance from the target previously chosen (or from the initial head position
in the case of the first peck) ;
c) the probability of a target's being chosen depends on its position with
respect to the orientation of the previous head-movement : targets that can
be reached as the result of a movement in the same direction as the previous
movement have a higher chance of being chosen than those requiring the move-
ment to take place in the opposite direction.

Principles b) and c) have to be examined more closely in order to lend
themselves to making a formal model.

In connection with b, the inverse of the square of the distance was the
function selected after testing the simplest function - the inverse of the
distance - on the data and finding it to be unsatisfactory. Using the square
of the distance suggests, therefore, that the time between 2 pecks ought to
be taken into account along with the distance between target locations. In
fact, by approximating head movements between two pecks by means of a symme-
trical movement that is subjected to uniform acceleration and then decelera-
tion, it is found that the energy expended in making this movement is propor-
tional to the square of the distance covered, provided the duration of the
movement is made to be constant.

In order to establish the theoretical probability distribution for the
first pecks, it is necessary furthermore to know the distance λ separating
the animal's head from the row of targets before the first choice is made.

Table II. Individual data, group data, and predicted values

a) First intake (N = 114)

Bird	*Target*									
	1	2	3	4	5	6	7	8	9	10
1	1	1	0	1	8	15	2	3	1	0
2	0	0	1	2	7	1	1	2	2	0
3	0	0	0	3	4	6	9	2	1	0
4	1	1	4	8	13	11	3	0	0	0
Group	2	2	5	14	32	33	15	7	4	0
Model	1.96	3.14	5.75	12.82	33.33	33.33	12.82	5.75	3.14	1.96

$$\chi^2_5 = 0.85, \; p > 0.95$$

b) Second intake following a central intake 5 or 6 (N = 65)

Bird	*Target*								
	1 or 10	2 or 9	3 or 8	4 or 7	6 or 5	7 or 4	8 or 3	9 or 2	10 or 1
1	1	0	3	9	6	0	3	0	1
2	0	0	3	3	0	1	1	0	0
3	0	1	1	6	1	1	0	0	0
4	0	0	2	13	7	1	1	0	0
Group	1	1	9	31	14	3	5	0	1
Model	1.80	3.21	7.22	28.86	12.83	5.50	2.82	1.67	1.10

$$\chi^2_3 = 0.78, \; p > 0.85$$

c) First sequence beginning with a central intake (N = 65)

Bird	5→1	5→2	5→3	5→4	5	5→6	5→7	5→8	5→9	5→10
1	3	0	4	2	8	2	1	2	0	1
2	1	0	0	2	5	0	0	0	0	0
3	1	0	3	2	3	0	1	0	0	0
4	7	0	1	5	4	2	2	1	0	2
Group	12	0	8	11	20	4	4	3	0	3
Model	9.44	1.49	5.36	12.57	23.31	5.73	2.79	1.21	0.28	2.81

$$\chi^2_3 = 1.62, \; p > 0.65$$

d) Number of sequences (N = 114)

Bird	*Number*									
	1	2	3	4	5	6	7	8	9	10
1	0	1	3	8	11	4	3	1	1	0
2	0	0	0	2	2	5	4	3	0	0
3	0	0	4	7	8	4	1	1	0	0
4	0	1	8	10	8	10	3	0	1	0
Group	0	2	15	27	29	23	11	5	2	0
Model	0.19	4.60	12.69	24.69	30.33	25.32	11.88	3.64	0.59	0.07

$$\chi^2_4 = 0.70, \; p > 0.95$$

The distance from the box to the target line is 1.5 cm. Better agreement between predictions and experimental data is however seen to be achieved by taking $\lambda = 1$ cm, which probably corresponds to the actual position of the head protruding through the aperture.

The probability p_1^i of the target is being chosen for the first peck is then given by :

$$p_1^i = f_{lin} \left(\frac{1}{d_i^2}\right) = \frac{\dfrac{1}{d_i^2}}{\displaystyle\sum_{j=1}^{j=10} \dfrac{1}{d_j^2}}$$

and :

$$d_j^2 = \lambda^2 + (j - 5.5)^2 \quad \text{for} \quad j = 1, 2, \ldots, 10.$$

The theoretical numbers given in Table IIa were calculated on the basis of these probabilities with $\lambda = 1$. It can be seen that there is excellent agreement with the data, and this is confirmed by the fact that χ^2 is far below the level of significance.

It is now proposed to return to principle c above, which will enable us to establish predictions for the subsequent pecks.

We apply this principle to an overall energy model and consider arbitrarily that a change of direction corresponds to a constant quantity ρ of energy used, converted here in distance units. Our model therefore still defines the probability p_i of a peck i being aimed at a target at a distance d_i from the target previously pecked, as being inversely proportional to the energy needed in order to reach this target.

This yields :

$p_i = f_{lin}\left(\dfrac{1}{d_i^2}\right)$ if the peck is made in the same direction as the previous movement,

and $p_i = f_{lin}\left(\dfrac{1}{d_i^2 + \rho}\right)$ if the peck is made in the opposite direction.

If we use I' to denote the set of remaining targets (i.e. those not yet taken) located in the same direction as the previous movement, and I" for the set of remaining targets in the opposite direction, the expression probability for a peck is as follows :

$$p_i = \cfrac{1}{d_i^2 \left(\overset{j \epsilon I'}{\underset{\Sigma}{}} \cfrac{1}{d_j^2} + \overset{j \epsilon I''}{\underset{\Sigma}{}} \cfrac{1}{d_j^2 + \rho} \right)} \qquad \text{for } i \epsilon I'$$

and

$$p_i = \cfrac{1}{(d_i^2 + \rho) \left(\overset{j \epsilon I'}{\underset{\Sigma}{}} \cfrac{1}{d_j^2} + \overset{j \epsilon I''}{\underset{\Sigma}{}} \cfrac{1}{d_j^2 + \rho} \right)} \qquad \text{for } i \epsilon I''$$

The theoretical numbers given in Tables IIb and IIc were calculated on the basis of the above probabilities. In this calculation, the value chosen for ρ (= 1.25) was the one that generally led to the best predictions. Tables IIb and IIc take into account only trials that began with a peck at targets 5 or 6. Given the symmetry of effects between targets 5 and 6 as starting points, trials beginning with either target 5 or 6 have been combined in these tables under the heading 5.

Once again, there is very good agreement between the predictions and the actual data, with regard to both the second peck considered separately (IIb), and the first sequences (IIc). It can be seen in particular that the asymmetry resulting from second pecks, which tend to favour the "smaller region", is well rendered by the model. This is proved by the values of the calculated χ^2.

In the context of Table IIc, our model also simulates another very spectacular effect, although this does not come into the calculation of the χ^2 : this is the lack of sequences culminating at the last-but-one target at each end of the row (i.e. sequences written 5 → 2 and 5 → 9). Behaviour consisting of never leaving an end-item uneaten can be explained in terms of a simple mechanism based on a proximity principle (cf. principle b of the model). There is no need to resort here to more complex strategies, by calculating for instance the total displacement needed in order to reach all the targets.

Lastly, let us consider an overall characteristic of pecking for which our model ought to account : the number of sequences that go to make up a trial. Table IId presents the theoretical values obtained by simulating our model by computers. Here again, there is excellent agreement between predictions and data, as if confirmed by the level of significance obtained for the calculated χ^2. It can be noted, moreover, that the mean theoretical distribution of the number of sequences, which is equal to 4.98, is only slight

ly different from the observed mean 5.04 (p $(t_{113} = 0.43) > 0.65)$.

Our probabilistic model is therefore capable of accounting for not only the characteristics of the first pecks, but also an essential characteristic of the whole set of pecks that constitutes a trial : the number of sequences that occurred. Figure 2 (dotted lines) summarizes all these predictions.

DISCUSSION

The model proposed was seen to be capable of predicting several aspects of pecking in young chicks, using only two parameters.

It should be noted, moreover, that one of these parameters (λ = initial distance from the animal's head to the row of targets) can be said to correspond to a physical parameter of the experimental situation.

As for the second parameter (ρ = energy required to effect a change of direction), although its value was determined a posteriori, the reference to energy, combined with the introduction of the square of the distance, opens an explanatory pathway in terms of the optimisation of pecking behaviour.

This approach is therefore along similar lines to other behavioural models dealing with foraging activities (e.g. "optimal foraging theory", see review by Pyke et al., 1977, and Krebs et al., 1981).

A "short-term" energetic approach does not provide us with a satisfactory explanation for our results, however. With our one-dimensional situation, it is easy to show that the most economical pecking patterns, from the point of view of the energy expended in motion, are those containing the smallest number of sequences. Ordered patterns (e.g., $1 \rightarrow 10$) and split patterns (e.g., $6 \rightarrow 10 - 5 \rightarrow 1$), which consist of one and two sequences respectively, are thus particularly economical in two respects : the total distance of head movement and the number of changes of direction. Thus, on the one hand it is clear from our results (cf. Fig. 6) that isolated young chicks do not spontaneously produce these optimal patterns[*]. However, on the other hand, these same results show, as we have seen, that pecking in young chicks cannot be held to be a matter of random even probabilities. Computer simulations show that patterns predicted by the model as well as observed patterns lead to a mean distance of head movement which is shorter than that due to a purely random pecking pattern.

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[*] A 2 month-old hen placed in similar experimental conditions was seen to frequently produce an ordered pecking pattern.

Pecking in young chicks therefore seems to present a compromise between a tendency to minimize the cost of head movements, and a tendency to conduct sampling among the set of targets available. The function of this sort of sampling in a natural environment could be to increase the chances of procuring a varied diet. This idea can be compared to other sampling policies in which immediate pairs are sacrificed in order to benefit in the long term (e.g. Houston, Kalcenik and McNamara, 1982 ; Oaten, 1977 ; McNamara, 1982). It is suggested that, as a probable result of a selective pressure, the chicks display this sampling behaviour in our homogeneous experimental setting, despite the fact that such a sampling procedure is not relevant in this particular situation.

Our model formalizes this compromise between the conservation of energy and the search for information. From this point of view, it is comparable to the approach of Krebs et al. (1978), who point to a balance between exploration and exploitation in great tits placed in a very different experimental situation from our own. Exploration and exploitation for Krebs et al. however correspond to two successive behavioural phases, whereas in our model the two functions occur simultaneously.

A final comment concerns the fact that this study does not elucidate the actual mechanisms responsible for the mode of pecking observed. Without attempting to specify the cause of the random variability governing the choice of a target, it is nevertheless possible to imagine relatively simple explanations for the inequalities of pecking probability. One needs only to assume, for instance, that the target's appearance in the chick's field of perception depends on the orientation of the animal's head and is inversely proportional to the square of the distance between them and the chick.

It would be very interesting to conduct further experiments from this standpoint, varying the arrangement of the targets and their distance from the chick.

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