# THE FEEDING FROM EDGE TOWARDS INNER PART IN SOYBEAN PLOT IN RUFOUS TURTLE DOVE, *STREPTOPELIA ORIENTALIS* (LATHAM) AND THE ESTIMATION OF PASSING RATE OF THE FLOCK

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## Introduction

Many birds enter the food sites from edge of them and moved into inner part, taking foods. Yamashita (1966) obtained the amount of food fed by the tree sparrow, *Passer montanus* Stejneger, on a feeder and found a behaviour feeding from outer to inner parts of feeder. Abe (1979) showed a similar behaviour in the rufous turtle dove, *Streptopelia orientalis* (Latham) which fed cotyledons of soybeans from the most outer row in the field. We have also observed the same behaviour in the same species in our experiments both in the fields and in the flight cage, where the injury intensity on soybeans by doves was to be estimated. Because of this behaviour, the injury by doves was not occurred evenly in a plot. Thus, we cannot obtain an accurate estimate of the rate of feeding until the distribution of injured plants, or the rate of passing in doves through plot, is given.

The rate of passing in birds may be affected by the number of birds entering the food site. It will increase with an increase in the number of individuals because of the interaction among individuals and of an increase of the amount of food fed by birds. In this paper, we attempt to estimate the rate of passing in *S. orientalis* in the soybean fields, by building a model expressing this behaviour. The results of the estimation will clarify the effect of the number of birds on the passing rate as well as the rate of feeding in doves on soybean plants.

## Methods

In order to know the seasonal fluctuations in the damage intensity by *S. orientalis*, soybean seeds were sowed biweekly in plots of 1 a in the experimental fields of the National Agriculture Research Center, Tsukuba, from mid-April to the end of August from 1980 to 1982 (Fig. 1). Two seeds were sowed at each hill on five rows of 40 m length, which were apart 50 cm each other. As the distance between hills was set as 20 cm, there were 200 hills in each row or 1,000 hills (or 2,000 seeds) in the whole plot. Each row was divided into 4 blocks with the same length, 10 m each, which were named
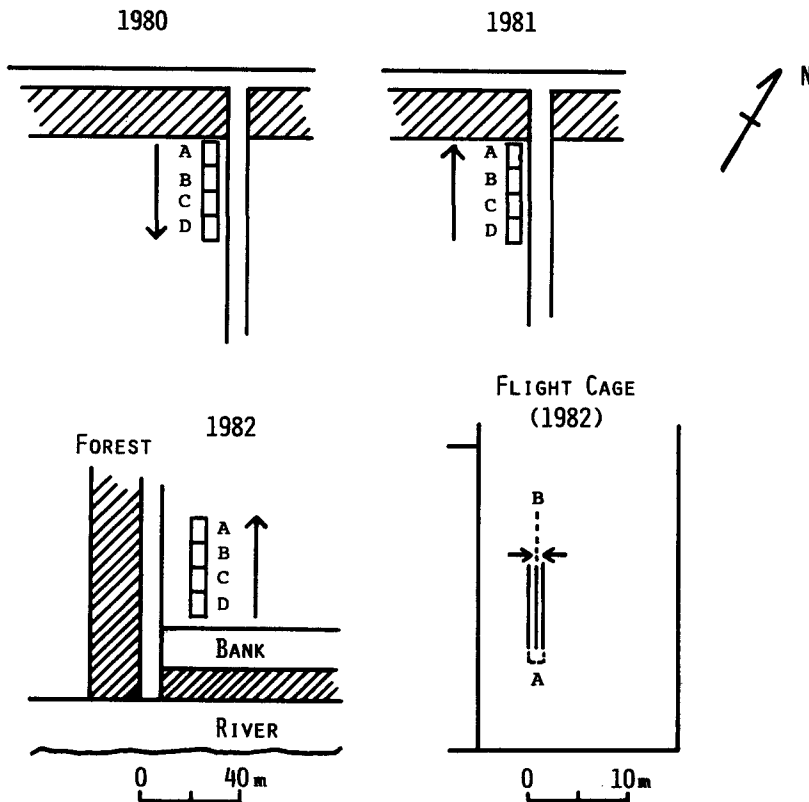
Fig. 1. The maps of experimental plots. A–D are the name of blocks and arrows show the direction from which doves are thought to enter the plot.

A, B, C and D. The number of soybean cotyledons appeared above the soil in each block in each row was counted every morning, observing whether or not the injury by doves was occurred.

Another experiment was conducted in a large flight cage, $40 \times 60 \times 12$ m high in 1982 (Fig. 1). In a plot within this cage two soybean seeds were sown in each hill, 20 cm apart each other, on three rows with a length of 8 m every two or three days for a total of six times. In this case, we set two blocks of the outer two rows and inner one without dividing each rows (Fig. 1). Seven doves were introduced into the cage, and the number of plants injured by doves was counted every morning and evening. A part of this experimental result was already reported by NAKAMURA and MATSUOKA (1983).

The number of plants injured by doves on the $j$th day from the emergence of cotyledons was converted into the ratio to the all plants available to eat for doves on that day, $f_i$. Doves cannot eat plants which grow too old to take as their foods. The mean time when plants reach this stage is 5 days after the beginning of cotyledon emergence (NAKAMURA and MATSUOKA, 1984). Therefore, the number of plants available to eat for doves on the $j$th day was calculated by subtracting the cumulative number of plants eaten by the $j$-1th day and that reaching 6 day old from the number of plants emerging by the $j$th day.

<center>RESULTS</center>

1.  The edge to inner part feeding in *S. orientalis*

Figure 2 shows the ratio of injured plants on each sequential day from the first to 5th after the beginning of cotyledon emergence, plotted against rows (Fig. 2A) and against blocks (Fig. 2B). This experiment was conducted in early May, 1982, and the almost all plants were eaten by doves finally. The ratio of injured plants increased gradually as the time passed, but there was little difference in it among rows (Fig. 2A). Contrarily, large difference was seen in the ratio among blocks (Fig. 2B): that is, while almost all plants in Blocks C and D were eaten, no plants in Block A on the first day. The ratio in Block A increased rapidly thereafter until it reached finally almost 1.0. This result shows that doves entered the plot from Block D and went towards Block A, eating the soybean plants.

The similar trend was observed also in all another experiments conducted here, except for both cases where the rate of feeding in doves was exceedingly high and low. In the former case, the time interval between observations of injured plants (i.e., one day) was too long to detect the trend.

The direction from which doves enter into the plot was shown in Fig. 1 for all experiments. In general, doves firstly perch on such objects as branches of trees and fences near plots and then, enter the plot after they look about carefully. Thus, doves show a tendency of entering the plot from the block near these objects. This was seen in the experiments in 1980 and 1982 (Fig. 1) where doves entered from the block most near to the forest for shelter (in 1980) or to the bank (in 1982). In the case of 1981, however, they entered the plot from Block D, which was an opposite part of the forest. Sometimes,
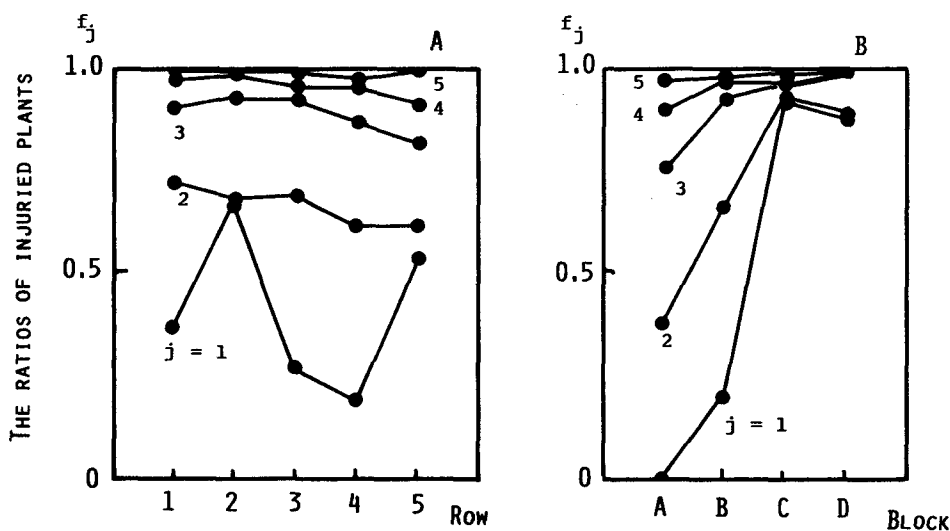


Fig. 2. The ratios of injured soybean plants in each row (A) and in each block (B) on the *j*th day after the emergence of buds.

feral pigeons, *Columba livia*, were observed in this year to come directly from the direction towards which Block D looked. They may affect more or less the unusual pattern of injury distribution in this year, but we have not found any reasons beyond it. In the experiments in the flight cage, doves always entered the plot from the outer rows into inner one.

### 2. A model for a passing feeding

In order to estimate the rate of passing, a simple model is constructed here. Let us assume that $n_0$ birds enter the area in which foods distribute evenly. This area is divided into $j$ blocks (Fig. 3). Thus, birds are to enter the area from Block 1 and go towards Block $j$.

Denoting the amount of food eaten in the $i$th block by time $t$ as $F_i$, it will be written as follows:

$$\Delta F_i = an_i \Delta t, \tag{1}$$

where $n_i$ is the number of birds entering that block *and* staying there during $\Delta t$, and $a$ the rate of feeding in an individual.

Next, assume that $n_i$ will be given as

$$n_i = bN_iE_i, \tag{2}$$

where $N_i$ represents the number of birds entering in the $i$th block in which they encounter food at the probability of $E_i$. Assume that a part of these birds, $bE_iN_i$, stay in that block and the other, $(1-b)E_iN_i + (1-E_i)N_i$, enter into the next block, and that the rate of staying, $b$, is constant in all blocks. Thus, the rate of passing rate is given as $1-b$. Therefore, eq. (1) is written as

$$\Delta F_i = abN_iE_i\Delta t. \tag{3}$$

If $g$ represents a mean area within which a bird detects one food, $E_i$ is given as $gD_i/S_i$, where $D_i$ and $S_i$ are the number of foods and the total area in the $i$th block, respectively. If $D_{m,i}$ represents the number of foods which occupies the whole area in the $i$th block (i.e., $D_{m,i} = S_i/g$), the probability at which a bird encounter food is given as

$$E_i = \frac{D_i}{D_{m,i}}$$
$$= \frac{D_{i0} - F_i}{D_{m,i}}, \tag{4}$$

where $D_{i0}$ is the initial number of food existing when birds enter the $i$th block.

As the number of birds entering the $i$th block, $N_i$, is $n_0 - \sum_{k=1}^{i-1} bN_kE_k$, we have the following equation if this term and eq. (4) are substituted to eq. (3):

$$\Delta F_i = abn_0\left(1 - \sum_{k=1}^{i-1}\frac{b}{n_0}N_kE_k\right)\frac{D_{i0}\left(1 - \frac{F_i}{D_{i0}}\right)}{D_{m,i}}\Delta t. \tag{5}$$
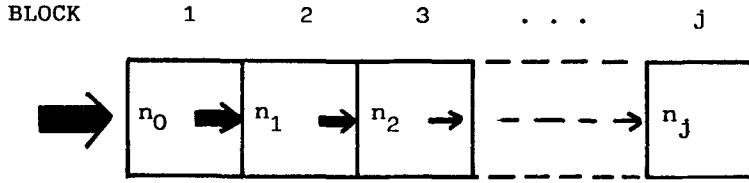
BLOCK    1    2    3   ...   $j$

Fig. 3. The blocks $(1, 2, ..., j)$ with an area in which foods are placed evenly and the number of birds entering each block (arrows). $n_0$ is the total number of birds visiting this area.

If $\Delta t$ approaches 0 in eq. (5), we have the following equation:

$$\frac{df_i}{dt} = \frac{1}{D_{i0}}\frac{dF_i}{dt}$$

$$= \frac{an_0 b}{D_{m,i}}\left(1 - \sum_{k=1}^{i-1}\frac{b}{n_0}N_k E_k\right)(1-f_i) \tag{6}$$

$$= \frac{an_0 b}{D_{m,i}}\left(1 - \frac{1}{an_0}\sum_{k=1}^{i-1}D_{m,k}\frac{df_k}{dt}\right)(1-f_i), \tag{6'}$$

where $f_i = F_i/D_{i0}$.

When $i=1$, we have following equation from eq. (6):

$$\frac{df_1}{dt} = \frac{an_0 b}{D_{m,1}}(1-f_1),$$

or

$$f_1 = e^{-(an_0 b/D_{m,1})t}, \tag{7}$$

if $f_1 = 0$ when $t=0$. This is equivalent to the equation of saturation.

These equations are held in the continuous feeding in short period in a day, but the feeding occurred continuously in several days, such as the experimental results obtained here, may be described by them as an approximation. In the latter case, we must adopt the following assumptions: the number of birds visiting food sites each day is constant in average and the interruption of feeding in the night does not affect the feeding in the next day.

Equation (6) was solved using an analog computer. Figure 4 shows an example of these solutions when an area in which food distributed evenly was divided into four blocks with the same size and 1.0 was given as a value of $b$. The curve of $f_1$ shows the saturation one in which the rate of increase decreases gradually until it becomes zero finally (eq. (7) ). The curve of $f$ in another blocks show an S-shaped ones; that is, the rate of increase increases gradually corresponding to the decrease in the number of food in outer blocks, and decreases as the number of food in that block approaches to zero.

If we take a ratio of $df_i$ to the same quantity in one of another blocks, say the $j$th one, $df_j$, we have the following equation from eq. (6):

$$\frac{df_i}{df_j} = \frac{D_{m,j}}{D_{m,i}}\cdot\frac{1-\sum_{k=1}^{i-1}\frac{b}{n_0}N_k}{1-\sum_{l=1}^{j-1}\frac{b}{n_0}N_l}\cdot\frac{1-f_i}{1-f_j}. \tag{8}$$
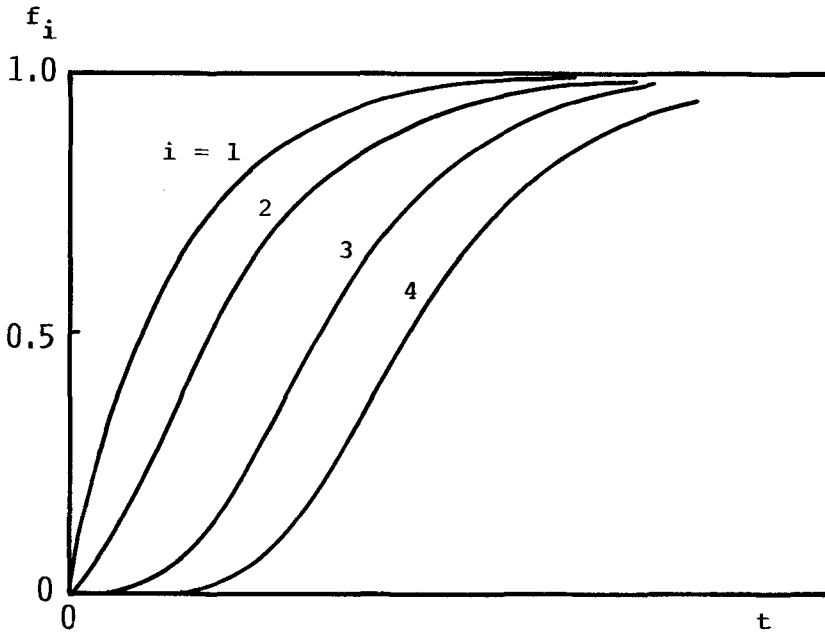
Fig. 4. The solution of eq. (6) when an area was divided into 4 blocks with the same size and 0.05 and 1.0 was given for $an_0$ and $b$, respectively. $f_i$ is the ratio of foods eaten in the $i$th block.

This equation shows that $df_i/df_j$ is dependent upon only one parameter, $b$, and independent of parameters, $a$ and $t$.

The values of $f$ in the 2nd, 3rd and 4th blocks obtained in Fig. 4 were plotted against those in the first one, $f_1$ (Fig. 5A). When the value of $b$ decreases, the concaveness in curves decreases (Fig. 5B), until curves become a straight line with an angle of 45° against the horizontal axis at $b=0$. This expression was firstly developed by YAMASHITA (1966)
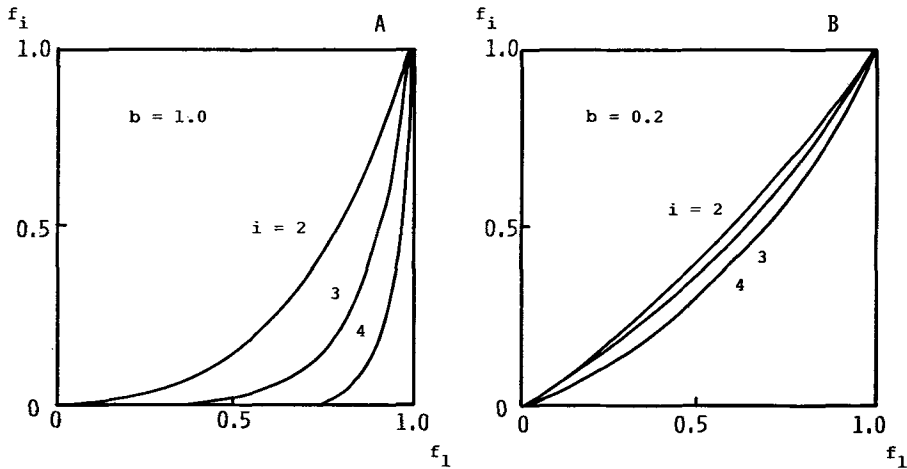


Fig. 5. The solution of eq. (8) plotted against $f_1$ (the ratio of food eaten in the first block) when 1.0 (A) and 0.2 (B) were given for $b$.

who analysed in the feeding behaviours of tree sparrows on a feeder. Since the shape of $f_i$ curves is determined only by the parameter $b$, this expression is convenient to know the largeness of $b$ from the experiment in which $f_i$ was not obtained sequentially, but did only at one time.

## 3. Estimation of values of $a$ and $b$

The values of $a$ and $b$ in the experiments were estimated using the model developed here. The block from which birds were thought to enter the plot was taken as the first one. Firstly, we assumed that $D_m$ was equal to the maximum number of soybeans in a block (i.e., 500). Then, substituting the values of $f_1$ obtained at the subsequent days to eq. (7), we obtained the value of $an_0 b$. Next, the value of $b$ was estimated by the following manner. Substituting the value of $an_0 b/D_{m,1}$ obtained above to eq. (6'), together with an arbitrary value of $an_0$, this equation was solved numerically using a computer to obtained $f_i$ for four each block ($i=1, 2, 3, 4$). Thus, ratios of $f_i$ to $f_j$ were computed for all 6 combinations among four blocks and these were compared with the values obtained in actual experiments. For a measure expressing the difference between both values, the value of $\chi^2$ was used here. This procedure was repeated, substituting new value of $b$ to eq. (6) given for the value of $\chi^2$ so as to be small, until the value of $\chi^2$ took a minimum one. Thus, the value of $an_0$ at this time was adopted as the final estimation for it. Dividing the value of $an_0 b$ by that of $an_0$, we had the value of $b$. In the experiments in the flight cage $a$ was obtained by dividing the values of $an_0$ by $n_0$ ($=7$).

Table 1 shows the results of these estimation, together with estimates of $an_0$ from the whole plot based on the pooled data of all blocks, disregarding the distribution of injured plants in the plot. The values of $an_0$ in the outdoor plots greatly fluctuated, depending upon the date of cotyledon emergence shown by NAKAMURA and MATSUOKA (1983). In

Table 1. The estimates of the rate of feeding in all doves visiting, $an_0$, and the rate of staying at a block, $b$, in experiments.

| Ex. No. | | Date* | $an_0$ | $a$ | $b$ | $an'_0$** |
|---|---|---|---|---|---|---|
| 11 | (1980) | May 15 | 8.230 | —— | 0.035 | 2.115 |
| 12 | (1980) | May 24 | 5.847 | —— | 0.035 | 0.315 |
| 13 | (1980) | June 7 | 0.168 | —— | 0.381 | 0.083 |
| 121 | (1981) | Apr. 28 | 0.180 | —— | 0.279 | 0.012 |
| 122 | (1981) | May 9 | 1.166 | —— | 0.180 | 0.799 |
| 13 | (1982) | May 17 | 40.838 | —— | 0.008 | 1.329 |
| 14 | (1982) | May 30 | 0.077 | —— | 0.331 | 0.032 |
| 61 | (F.C.) | Aug. 14 | 0.143 | 0.020 | 0.176 | 0.094 |
| 62 | (F.C.) | Aug. 15 | 0.371 | 0.053 | 0.177 | 0.317 |
| 63 | (F.C.) | Aug. 17 | 1.426 | 0.204 | 0.118 | 0.631 |
| 64 | (F.C.) | Aug. 20 | 0.942 | 0.135 | 0.178 | 0.444 |

* The first day on which the cotyledons appeared.

** The estimates of $an_0$ from the whole plot based on the pooled data of all blocks. F.C. is the experiments in the flight cage.
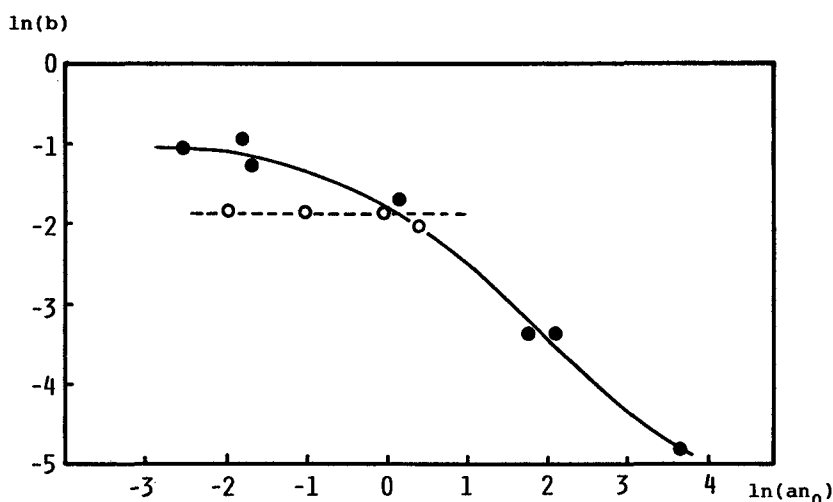
ln(b)



Fig. 6. The relationship between values of $an_0$ and those of $b$ estimated from experiments in outdoor plots (solid circles) and in plots in the flight cage (open circles).

the experiments conducted in the flight cage (Ex. 61–64), the values of $an_0$, (or $a$), increased with the sequence of experiments.

The value of $b$ in the field experiments also fluctuated greatly, correlating negatively with the values of $an_0$. However, those in the experiments in the cage, having a constant $n_0$, showed almost constant (Fig. 6).

## DISCUSSION

It was shown here that *S. orientalis* enters the soybean plot from the edge and goes towards the opposite edge, feeding the plants (Figs. 1 and 2). Similar behaviour was already observed in the same species (ABE, 1978), the tree sparrow, *Passer montanus* (YAMASHITA, 1966) and the chukar, *Alectoris chukar* (BENJAMINI, 1980). KIDOKORO (1984) showed that the injury of matured rice plants by the spot-billed duck, *Anas poecilorhyncha*, occurred only in a narrow part bordered of paddy fields. All tese species except for sparrow enter into food sites by walking, suggesting that they walk inwards feeding foods encountered on their path. As a result, the injury extends from an edge to inner parts of a plot.

Because of this behaviour, the distribution of injured plants in the plot does not show random or even ones, but a gradient from the edge of plot from which birds entered to the center or the opposite edge of the plot. This distribution pattern affects greatly on the estimation of the damage or on the rate of feeding in birds (or the intensity of injury). The rate of feeding estimated disregarding the distribution pattern in injured plants ($an'_0$ in Table 1) was always underestimate of $an_0$ and the bias becomes larger as the value of $an_0$ increases (Table 1).

Since $an_0$ is the product of the rate of feeding in individuals, $a$, and the number of

birds in the flock, $n_0$, we can call $an_0$ as the rate of feeding in *flock*. In the experiments in the field, we cannot obtain the value of $a$ until the mean number of birds in flock visting the plot is estimated accurately. Contrarily, those are possible to be obtained in the experiments conducted in the flight cage (Ex. 61–64 in Table 1) where a constant number of doves was kept ($a$ in Table 1). The values of $a$ estimated increased with the sequence of experiments, suggesting that the doves became to acclimate a new food and/or new food place, as already discussed by NAKAMURA and MATSUOKA (1983). The fluctuation in the values of $an_0$ in the field experiments must be caused by the fluctuations of both values of $a$ and $n_0$. Of these, the fluctuation in the former ($a$) is resulted mainly from the change in the acclimation of new foods and that in the latter ($n_0$) caused through the change in the preference in doves to soybeans, which is partly determined by the relative amount of soybeans to the whole foods available to doves (NAKAMURA and MATSUOKA, 1983).

However, the effect of acclimation on $an_0$ seems to be small in the field experiments conducted here, because the values of $an_0$ always decreased with the passage of time except for the experiments in 1981 (Table 1), contrary to the expected effects of acclimation. If this is true, we can say that the fluctuation in $an_0$ in the field experiments is mainly due to the seasonal fluctuation in $n_0$.

The values of $b$ (the rate of staying in a block in birds) in the field experiments decreased as the values of $an_0$ increased, though those obtained in the cage was almost constant, irrespective of $an_0$ (Fig. 6). Since $n_0$ was constant in the cage, we can say from this result that $b$ is independent of $a$. Therefore, the result obtained in Fig. 6 shows that the values of $b$ decrease with an increase in $n_0$, since the largeness in $an_0$ in the field experiments is thought to reflect that in $n_0$, as discussed above. In other words, doves pass blocks at higher rate when more doves visit the plot. This phenomenon is probably caused by an aggresive behaviour of dominant dove to subordinate ones. Truly, it is often observed in the field that doves coming to the food place are driven out by the individual which occupied it.

It is natural that the foraging in *S. orientalis* extends from an edge of the plot because of their behaviour of entering the plot by walk. However, higher damage of wheat by tree sparrows and that of brassica by the brown-eared bulbul, *Hypsipes amaurotis*, often occur in border parts in the plot (NAKAMURA's unpublished data). Since these species come directly on the feeding site in the plot, these foraging behaviour will distribute widely in many species of birds. Thus, the foraging behaviour from an edge of the plot may have an adaptive significance of easily retreating into the hiding-places from predators.

Observations on foraging behavior in the captive *S. orientalis* in a flight cage (MATSUOKA's unpublished data) show that dove's feeding flock is local enhancement (CROOK, 1965): that is, when one bird comes down the ground, others join in feeding. This behaviour is thought to increase the rate of energy return on investiment by avoiding the searching a place that has been already harvested by other birds (ALCOCK, 1979).

We must clarify the adaptive significance of the feeding from an edge in future.

The passing rate, $1-b$, will be a useful parameter when we want to know the spread of injury in the plot, as in the case where the effects of some stimuli on the scaring the pest birds are compared in the field. These will be discussed in another place.

## SUMMARY

Rufous turtle dove, Streptopelia orientalis, coming to the soybean field entered it from the outer part to eat soybean cotyledons. As a result, the injured plants extended from the outer to inner parts in the field. A model expressing these behaviours was constructed here, by assuming that the amount of food birds can eat in one block determines whether they stay there or move into neighbour block. As the food decrease due to exploitation of them by birds, birds enter into farther parts with the passage of time.

The rate of feeding in all visiting birds ($an_0$ where $a$ is the rate of feeding per individual and $n_0$ the number of birds visiting) and the rate of staying at a block, $b$, was estimated from the field experimental results, using the above model. The value of $an_0$ fluctuated greatly, depending upon the season in which soybean seeds sowed. The value of $b$ also fluctuated inversely with that of $an_0$, suggesting that the staying rate decreases with an increase in the number of doves coming, probably because of interference among individuals.

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# キジバトに見られたダイズ畑の縁から内部へ向かう採食と群れの通過率の推定

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　ダイズの播種圃場を訪れて採食するキジバトは，縁から内部へ向かって歩きながら採食する行動が見られた．その結果，キジバトによる加害は，ハトの侵入した圃場の縁から反対方向へ向かって拡がっていく傾斜のある分布を示した．このため，圃場内のハトの通過率を推定しない限り，ハトの採食率を正確に推定することができない．

　そこで，餌場の縁から内部へ向かって採食しながら進んでいく行動を表わすモデルを作って，採食率の推定を行った．このモデルでは，鳥があるブロックに留まるか，それとも隣りのブロックへ移動するかは，そのブロック内に残っている餌の量と餌や場所の選好度などによって決まる滞在率 ($b$) とによって決定されると仮定された．野外と網室内で得られた実験結果をこのモデルに適用させることで，畑を訪れたハトの群れの採食率 ($an_0$) と滞在率とを推定した．$an_0$ の値はダイズを播種した季節によって大きく変動した．また，$b$ の値は $an_0$ が大きいときには小さく，小さいときには大きくなる傾向を示した．$an_0$ の変動は，主として畑に訪れたハトの個体数 ($n_0$) に依存していると考えられるから，ハトの個体数が多いとき $b$ の値は小さくなるといえる．これは，個体数が多くなるに伴って個体間の干渉が強まることによるものと思われる．