Some Mathematical Considerations
on Two-mode Searching I

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Purpose of this paper is to consider mathematically the relation between the efficiency of two-mode searching behavior and the target's patchy distribution. Two-mode searching includes patch-searching and target-catching. Two intuitive models are presented: Model 1 constructed by a Wiener process on $\mathbf{R}^1$; Model 2 by a time-discrete Markov process on $\mathbf{S}^1$, that is, on a circle. These two different models give different results depending on the characteristics of each model. We apply our results to a coevolutionary game between the searcher's searching behavior and the target's distribution. Compared with a simple mode searching, the superiority of two-mode searching is shown to depend seriously on the target's distribution.

Key words: searching, mathematical model, Wiener process, Markov process

1. Introduction

It is well-known that various species of insects behave in a two-mode way to search the target (e.g., food, mate, or host) distributed patchily in space. Such a behavior is frequently called "area-concentrated search". An insect searches a patch of targets with a relatively large motion which is adaptable to the spatial scale of patch distribution; then, after finding the first target, it reduces its scale of motion to search another target in a relatively near region. Successively, obeying some criteria, the searcher re-changes its behavior to search another patch. Such a criterion typically belongs to one of the following three types: (a) fixed-time strategy, i.e., the searcher stays for a fixed period of time in each patch encountered; (b) fixed-number strategy, i.e., the searcher stays until it catches a fixed number of targets in each patch encountered; (c) fixed-giving up time strategy, i.e., the searcher stays in each patch encountered as long as the time interval between a catch and the next catch does not exceed a fixed value. A variety of mathematical models have contributed to the understanding of such a behavior within the framework of evolutionary strategy (Murdie [10], Murdie and Hassel [11], Cowie and Krebs [2], Iwasa et al. [5], Knoppien and Reddingius [8]).

In this paper, we shall mathematically demonstrate that a two-mode searching may become an adaptable strategy of searcher in a coevolutionary game between the searching behavior and the target's distribution. The searcher is assumed to behave always to realize the possible highest mean searching efficiency. If the target distribution is assumed to be directed to make the efficiency as low as possible, this

coevolutionary game can be called a minimax game between the searcher and the target (Stewart-Oaten [16]). If the distribution is assumed to be directed to make the mean efficiency as high as possible, this game can be regarded cooperative. We shall call the former type of target "the counter-behaving target" and the latter "the cooperative-behaving target".

We shall deal with two analytically tractable models on a one-dimensional space: Model 1 constructed by a Wiener process; Model 2 by a time-discrete Markov process. Though the purpose of modelling is the same, they should be independently considered because of the difference between the underlying assumptions. Indeed, the performed analysis will disclose that some features are very interestingly different between two models.

2.   Modelling Assumption

Target: Both patches and targets are respectively assumed to be uniformly, that is, regularly distributed on the space and in the patch, and all identical to each other. We set ΔS the distance between the nearest-neighbor patches and ΔL between the nearest-neighbor targets and l the length of patch zone (the possible longest distance between two targets in a patch). Each patch contains N individuals of target. Thus, it is naturally assumed that $N\Delta L = l$. These assumptions may seem to be too ideal, compared with other models that take into account the qualitative difference among patches (e.g., Iwasa et al. [5]). But, purpose of our models is to demonstrate mathematically the set-up of a coevolutionary game between the searcher's searching behavior and the target distribution. As a starting point of a mathematical consideration, such a simplification should be allowed. Moreover, to consider some real phenomena or more sophisticated models, it is frequently worth while knowing what results are implied from such simple models.

In almost all the previous papers, the target distribution has not been considered as a strategy available or beneficial for the target against the searcher's searching, while it has been one of environmental factors which have an effect on the searching efficiency. Moreover, for instance, it may be very easy to accept the assumption that each counter-behaving target takes the position to minimize the *risk* to be found, such as in selfish herd of Hamilton [4], than the assumption of minimizing the *total* searching efficiency. In this paper, we can consider as follows: Considered targets are offsprings of a single parent individual who chooses the dis-

tribution. In the prey-predator relation, the lower searching efficiency contributes to the higher survival rate of offspring, consequently to the higher inheritance rate of its parent's gene. Another way to consider is that targets located in a patch are strongly related to each other and by kin selection mechanisms each target behaves on the benefit of the total, that is, depending on the total searching efficiency. The former may correspond to the case when targets are immobile eggs, while the latter to the case when they are a kind of movable juveniles.

We shall assume a restriction for the target distribution: The area available for the target distribution is limited. Thus, the larger is the size of patch, the smaller is the distance between patches. Moreover, the larger is the size of patch, the larger is the distance between targets for a fixed number of targets in the patch. In this paper, this restriction is assumed to be given by:

$$(\text{H}) \qquad\qquad \Delta S + N \Delta L = A,$$

where A can be regarded as a given share of space per patch. The target must select its distribution pattern under this restriction. As for a prey-predator relation, it is very likely that the prey distribution may be restricted by the spatial resource distribution. For example, when a plant is the prey, it may be restricted by light intensity, humidity, etc. When the preys are a kind of insects settling or eggs laid on a plant, it is obviously restricted by the available area on the plant.

We shall also take account of the target size, say b. The existence of a non-zero target size excludes that the patch size can be zero. That is, when we discuss the effect of the target size, the size will be seen to play a role in restricting the target's selection of ΔL: More precisely $b \leq \Delta L$. The size b may be regarded as a minimal necessary share of space per target, too.

Searcher: In our model, the searcher's searching consists of two processes on a one-dimensional space: patch-searching process and target-catching process. In each process, the searcher is viewed as a point moving on the space. The switching rule between two processes is as follows: The patch-searching process is terminated when the searcher encounters a certain point or enters a certain region of the given space. It is regarded as the moment when the searcher finds a patch and catches a target. On the other hand, the target-catching process continues from this moment until the searcher's gain satisfies a given criterion in this process.

The searching efficiency E is defined as follows:

$$E \equiv \frac{M}{T_1 + T_2},$$

where T_1 denotes the time taken in the patch-searching process, T_2 the time taken in the target-catching process for catching M targets. A higher efficiency means a better searching behavior for the searcher. We shall investigate the optimal strategy to realize the highest efficiency for a fixed patch's quality (distances between nearest-neighbor patches and between nearest-neighbor targets). As mentioned above, since a functional relation between the target density in the patch and the patch size will

be hypothesized, the efficiencies of searching a patch and of catching targets in a patch are not independent. In some previous analytical models, it seems that there was little consideration on a relation between the easinesses of finding a patch and of catching a target within a patch, that is, on a functional relation between T_1 and T_2. For example, the time T_1 was assumed to be independent of T_2 and was averaged with respect to a stochastic ensemble (Iwasa et al. [5]). Taking such a relation into consideration, others tried to discuss a relation between the prey distribution and the predator's searching strategy (e.g., Cain [1]), though their models were not analytically tractable but computer-simulated.

We shall not make any assumption on the size of the searcher, though it may be possible to introduce such a searching capacity like the disc model (Koopman [9], Paloheimo [13], [14], Royama [15], Nackman [12]). Searching is assumed to be independent of the searcher's size and only depending on its searching capacity (for example, the sensibility of sensillum).
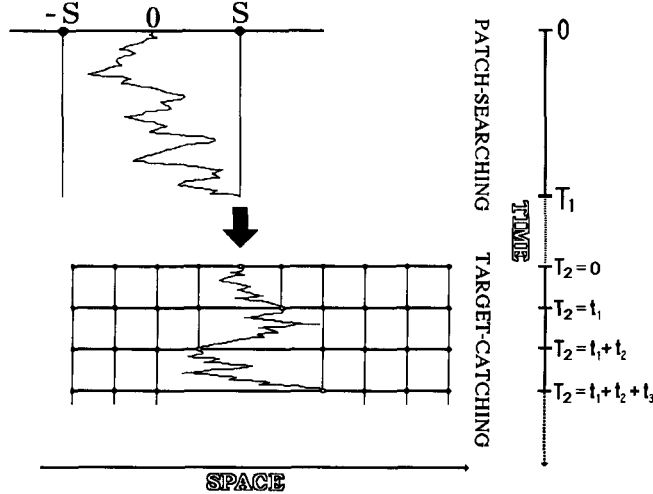

Fig. 1. Scheme of Model 1. Model consists of a patch-searching process and a target-catching process. These processes are modeled with two independent Wiener processes of the infinitesimal variance σ_1^2 and σ_2^2 respectively. For a more detailed explanation, see the text.

3. Model 1

Model 1 is considered on a one-dimensional space $\mathbf{R}^1$ (Fig. 1). In each of two processes, the searcher is assumed to be a point moving continuously on $\mathbf{R}^1$ as a Wiener process, that is as a Brownian motion (about which, for example, see Cox and Miller [3]). Moreover, we shall assume that there is no drift, which means that the searcher moves completely at random without any biased direction. Wiener process may be a zero-th approximation of the real movement. As shown in Fig. 1, the patch-searching process is terminated when the searcher encounters a point on $\mathbf{R}^1$. On the same moment, the searcher finds a target within a patch. On the other hand, the target-catching process continues from this moment until

the searcher catches targets whose number is given as a searcher's strategy, say M. This assumption means that the searcher takes a "fixed-number" strategy. We shall see that the efficiency E is a function of M and show that there can exist a unique M, say M^*, which realizes the highest mean efficiency for a fixed patch's quality. The searcher's strategy is identified with the number M of caught targets. And the searcher is assumed to take always the optimal value $M = M^*$ for any fixed ΔS and ΔL.

We shall not appeal to the infinitesimal variance of Wiener process as the searcher's strategy. Trivially, in our model used Wiener process, a larger variance always results in a shorter mean first-passage-time, and consequently in a higher efficiency. But, naturally since the searching velocity cannot become infinitely large, the variance is assumed to be a finite constant which simply expresses a characteristic of searcher's random motion. It is implicitly assumed that the variance for the patch-searching process is greater than that for the target-catching process, because the patch size is in general relatively small compared to the space scale with which patches are distributed.

Patch-Searching Process: For this process, we shall assume the Wiener process with infinitesimal variance $\sigma_1{}^2$. The searcher is assumed to begin its search at the origin on $\mathbf{R}^1$ (Fig. 1). Two points are set at $x = -S$ and $x = S$ as nearest-neighbor two patches. Thus, $\Delta S = 2S$. It may seem to be more natural to consider that the starting point is randomly distributed out of a patch. But the starting point is not important to discuss the searching efficiency in our following argument. Indeed, even if the starting point was taken into consideration, it would contribute only as a constant which does not affect our arguments. Moreover, supposed that the starting point is uniformly distributed (this is a natural assumption and the searcher does not know the position of the patches at all), the mean starting point is located at the center between the two patches.

The moment generating function (m.g.f.) of T_1 is given by that of the first-passage-time with symmetric absorbing boundaries (L.M. Ricciardi, private communication):

$$(1.1) \qquad G_\lambda = \operatorname{cosech}\left[\frac{\Delta S}{\sigma_1}\sqrt{\frac{\lambda}{2}}\right].$$

From this m.g.f., we can obtain the mean time $\langle T_1 \rangle$:

$$(1.2) \qquad \langle T_1 \rangle = \left[-\frac{\partial G_\lambda}{\partial \lambda}\right]_{\lambda=0} = \left(\frac{\Delta S}{2\sigma_1}\right)^2.$$

Target-Catching Process: The searcher is assumed to catch one target at $T_2 = 0$, that is, at the moment when the searcher begins the target-catching process. The searcher searches the next neighbor target by the Wiener process with an infinitesimal variance $\sigma_2{}^2$ which is less than $\sigma_1{}^2$. The caught target is assumed to be removed. Thus, after repeatedly targets are caught, there will be a wide region

with no target (see Fig. 1). We do not necessarily consider this removal as target's absolute disappearance, instead can consider it as its quality change to become useless for the searching searcher so that, for example, the target may be regarded as the host undergone the polyparasitism. In this case, the removed target for a searcher is the existing and useful target for another.

Since the searcher undergoes the Wiener process in this region, the mean period $\langle t_j \rangle$ for catching the $(j+1)$-th target after the j-th is shorter than $\langle t_{j+1} \rangle$ for catching the $(j+2)$-th after the $(j+1)$-th. The m.g.f. of period t_j for catching the $(j+1)$-th target after the j-th one is given by that of the first-passage-time with absorbing boundaries at $x = \Delta L$ and $x = j\Delta L$ (L.M. Ricciardi, private communication):

$$(1.3) \qquad g_{\lambda,j} = \frac{\sinh\left[j\frac{\Delta L\sqrt{2\lambda}}{\sigma_2}\right] + \sinh\left[\frac{\Delta L\sqrt{2\lambda}}{\sigma_2}\right]}{\sinh\left[(j+1)\frac{\Delta L\sqrt{2\lambda}}{\sigma_2}\right]}.$$

Then, the mean time $\langle t_j \rangle$ is given by:

$$(1.4) \qquad \langle t_j \rangle = \left[-\frac{\partial g_{\lambda,j}}{\partial \lambda}\right]_{\lambda=0} = j\left(\frac{\Delta L}{\sigma_2}\right)^2.$$

Lastly, we can find the mean time $\langle T_2 \rangle$ to catch M targets:

$$(1.5) \qquad \langle T_2 \rangle = \left\langle \sum_{j=1}^{M-1} t_j \right\rangle = \sum_{j=1}^{M-1} \langle t_j \rangle = \frac{1}{2}\left(\frac{\Delta L}{\sigma_2}\right)^2 M(M-1).$$

Here note that t_j and t_k $(j \neq k)$ are independent to bring the above second equality.

Efficiency: Making use of the above results, we can find the mean efficiency:

$$(1.6) \qquad \langle E \rangle_M = \frac{M}{\langle T_1 \rangle + \langle T_2 \rangle} = \frac{M}{\frac{1}{4}\left(\frac{\Delta S}{\sigma_1}\right)^2 + \frac{1}{2}\left(\frac{\Delta L}{\sigma_2}\right)^2 M(M-1)}.$$

The sub-index M indicates that the searcher takes a strategy with the behavior-switching number M.

Analysis: Calculating $\partial\langle E \rangle_M / \partial M$, we find that there is a unique M^*, which maximizes the mean efficiency:

$$(1.7) \qquad M^* = \frac{1}{\sqrt{2}}\frac{\Delta S}{\Delta L}\frac{\sigma_2}{\sigma_1}.$$

Note that M^* is a real number, whereas the searcher can take only a positive integer number as the behavior-switching number. If this M^* is less than or equal to 1, the available optimal behavior-switching number of the searcher is obviously 1. Further, even when $1 < M^* < 2$, the searcher must take the behavior-switching number 1 if the efficiency for $M = 1$ is higher than that for $M = 2$ (i.e., $\langle E \rangle_2 < \langle E \rangle_1$). By this argument, we prove the following lemma:

LEMMA 1.1. *If*

(1.8)
$$\frac{1}{2}\frac{\sigma_2}{\sigma_1} < \frac{\Delta L}{\Delta S},$$

then, the searcher's optimal behavior-switching number is 1 (that is, the searcher's optimal behavior is not to use any two-mode searching but to search with a simple mode).

(1.8) means also that $M^* < \sqrt{2}$. Unless (1.8) is satisfied, a two-mode searching can realize the highest mean efficiency with an optimal behavior-switching number, say M_{opt}, which is a unique positive integer $[M^*]$ or $[M^*] + 1$. Here $[M^*]$ means the largest integer less than or equal to M^*. As the qualitative result is the same, for mathematical convenience we shall hereafter focus on the case when $M = M^*$ instead of $M = M_{\text{opt}}$. When $M = M^*$, the efficiency is given as:

(1.9)
$$\langle E \rangle_{M^*} = \sqrt{2} \left\{ \frac{\Delta L}{\sigma_2} \left(\frac{\Delta S}{\sigma_1} - \frac{1}{\sqrt{2}} \frac{\Delta L}{\sigma_2} \right) \right\}^{-1}.$$
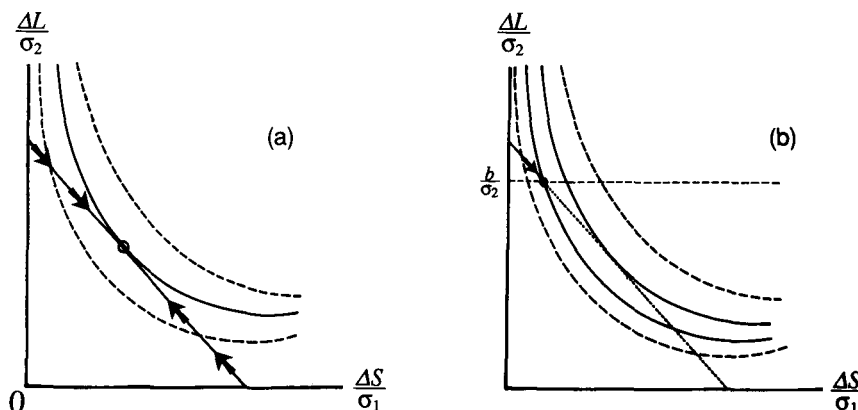

Fig. 2.   Coevolutionary game between the searcher and the counter-behaving target: a) $b = 0$; b) $b > 0$. The game reaches its equilibrium at a point indicated as a circle in the figure. Arrows show the direction of strategy change of target. In case of the cooperative-behaving target, the direction is opposite. The target distribution is restricted on a line. Curves respectively correspond to different searching efficiencies depending on the searcher's behavior-switching number. Upper curve has a lower efficiency. In (b), shown is the case when the effect of target size changes the equilibrium differently from that in (a).

Note that, as shown in Fig. 1, the target-catching process is assumed to start from a point middle in a patch. If M^* is greater than the number of targets in a patch N, our previous results are not applicable. Indeed, if $N \leq M^*$, the searcher certainly goes out of the patch in the target-catching process, when one of nearest-neighbor targets is located with a distance more than ΔS. Taking account of such

a situation is mathematically very complicated. Our above calculation about the target-catching process is obviously valid only when $M^* < N$. Further, even when $M^* < N$, if the searcher catches the target at the edge of patch during the target-catching process, from that moment our calculation for the target-catching process is not applicable. Thus, here we can reliably consider only the case when the number of targets in a patch is so large that $M^* < N$ and the searcher cannot reach the edge of a patch before catching M^* targets.

i) $b = 0$: At first, we consider the case when the target size is negligible, that is, there is no target size effect. In this case the lower bound for ΔL is zero. Fig. 2(a) shows the behavior of (1.9) for some values of $\langle E \rangle_{M^*}$ and that of (H) for a set of parameters σ_1, σ_2, N, and A. The target must select its distribution pattern only on a unique line appeared in Fig. 2(a).

In case of the counter-behaving target, the coevolutionary game leads to a tangential point between (H) and (1.9) as shown in Fig. 2(a), where the behavior confliction between the searcher and the target is balanced. By means of (1.9), it is easily seen that such a tangential point always exists and is unique. The point gives the following strategic goal:

$$(1.10) \qquad \Delta S^* = A \cdot \frac{\sqrt{2} + N\sigma_2/\sigma_1}{\sqrt{2} + 2N\sigma_2/\sigma_1}$$

$$(1.11) \qquad \Delta L^* = A \cdot \frac{\sigma_2/\sigma_1}{\sqrt{2} + 2N\sigma_2/\sigma_1}$$

$$(1.12) \qquad M^* = \sqrt{2} + \frac{\sigma_2}{\sigma_1} N.$$

As obviously seen that $\sqrt{2} > M^*$, we obtain the following result, applying Lemma 1.1 to the above coevolutionary goal ponit:

RESULT 1.1.   *At the coevolutionary goal in case of the counter-behaving target with negligible body size, two-mode searching behavior is always adopted versus the targets' patchy distribution.*

On the other hand, in case of the cooperative-behaving target, the following result can be easily obtained by inverting those arrows in Fig. 2(a) and using Lemma 1.1:

LEMMA 1.2.   *When the target size is negligible in case of the cooperative-behaving target, if*

$$\Delta L^* < \Delta L_0,$$

then the coevolutionary goal consists of the target's uniform distribution in space and the searcher's simple mode searching. Otherwise, the goal consists of the target distribution as patchy as possible and the searcher's two mode searching.

ΔL_0 denotes a selected distance between nearest-neighbor targets at the initial of game. ΔL^* is given by (1.11). We obtain Fig. 4. From the figure, further we can see

that, if $A \leq 4\Delta L_0$, then the coevolutionary goal always consists of a simple mode searching versus the targets' uniform distribution. This is because, if $A \leq 4\Delta L_0$, the region for the two-mode searching is contained in the region where $N \leq 2$ in Fig. 4. Any two-mode searching with $N \leq 2$ is always nonsense. We obtain the following results from Fig. 4:
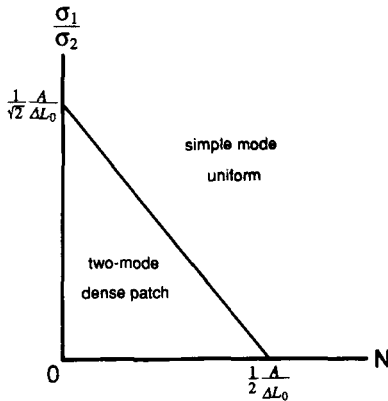

Fig. 3. Coevolutionary goal when $b = 0$ in case of the cooperative-behaving target. Even when $b > 0$, if $\sqrt{2}b \leq \Delta L_0$, then the result is the same. In case of "dense patch", every nearest-neighbor targets touch each other in the patch.
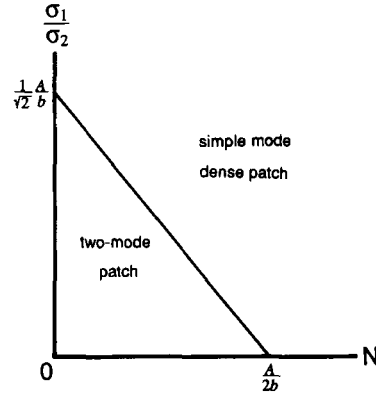
Fig. 4. Coevolutionary goal when $b > 0$ in case of the counter-behaving target.

RESULT 1.2. *At the coevolutionary goal in case of the cooperative-behaving target with negligible body size, if the target density is sufficiently low in the patch at the initial of coevolutionary game, a simple mode searching behavior is adopted versus the targets' uniform distribution.*

RESULT 1.3. *At the coevolutionary goal in case of the cooperative-behaving target with negligible body dize, in order that a two-mode searching behavior is adaptable versus the targets' patchy distribution, the target density must be sufficiently high in the patch, and the patch size must be sufficiently small. The adopted two-mode searching has a relatively moderate change of behavior.*

Here, for the searcher's behavior, we used the word "moderate" to mean a small difference between σ_1 and σ_2 under the condition that $\sigma_2 < \sigma_1$.

ii) $b > 0$: The patch size cannot become less than bN. When the patch size is bN, every nearest-neighbor targets touch each other with no gap. This restriction of patch size is likely to change the coevolutionary goal shown by (1.10), (1.11) and (1.12). As easily seen from Fig. 2(b), if and only if $b \leq \Delta L^*$, those results are valid even when $b > 0$ in case of the counter-behaving target:

Lemma 1.3.   *When the target size is not negligible in case of the counter-behaving target, if*

$$(1.13) \qquad\qquad N \leq \frac{A}{2b} - \frac{1}{\sqrt{2}} \frac{\sigma_1}{\sigma_2},$$

the coevolutionary goal is given by (1.10), (1.11) *and* (1.12).

As for the case of the cooperative-behaving target, we obtain:

Lemma 1.4.   *When the target size is not negligible and the condition* (1.13) *is satisfied in case of the cooperative-behaving target, if*

$$\Delta L^* < \Delta L_0,$$

then the coevolutionary goal consists of the target's uniform distribution in space and the searcher's simple mode searching. Otherwise the target distribution is as patchy as possible, so that every nearest-neighbor targets touch each other. Then the searcher's behavior is:

a simple mode searching when $\sqrt{2}\frac{\sigma_1}{\sigma_2} + 2N \leq \frac{A}{b} < 2\frac{\sigma_1}{\sigma_2} + N;$

a two-mode searching when $2\frac{\sigma_1}{\sigma_2} + N < \frac{A}{b},$

where we used Lemma 1.1 *and the assumption* (H). ΔL^* *is given by* (1.11).

Next, we consider the case when the coevolutionary goal in case of the counter-behaving target is different from the previous result due to the target size effect. In Fig. 2(b), we show such a situation. If (1.13) is unsatisfied, the coevolutionary goal expressed by (1.10), (1.11), and (1.12) is not attainable. The substituted goal is expressed as follows:

$$(1.14) \qquad\qquad \Delta S^* = A - bN$$

$$(1.15) \qquad\qquad \Delta L^* = b$$

$$(1.16) \qquad\qquad M^* = \frac{1}{\sqrt{2}} \frac{\sigma_2}{\sigma_1} \left(\frac{A}{b} - N \right).$$

By virtue of Lemma 1.1, in the same way as before, we obtain Fig. 4 and Fig. 5 via Lemmas 1.3 and 1.4. From Fig. 4, we can easily find that, when $0.25 \leq b/A$, a simple mode searching is always adopted versus the targets' patchy distribution:

Result 1.4.   *Even when the target size is not negligible in case of the counter-behaving target, if it is sufficiently large compared to the available total area per patch, the coevolutionary goal consists of a simple mode searching behavior versus the targets' patchy distribution.*

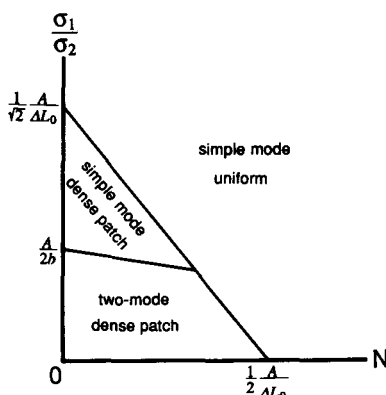As for the adaptability of two-mode searching, we obtain:

Fig. 5.   Coevolutionary goal when $0 < b \leq \Delta L_0 < \sqrt{2}b$ in case of the cooperative-behaving target. When $\sqrt{2}b \leq \Delta L_0$, the result is the same as Fig. 3.
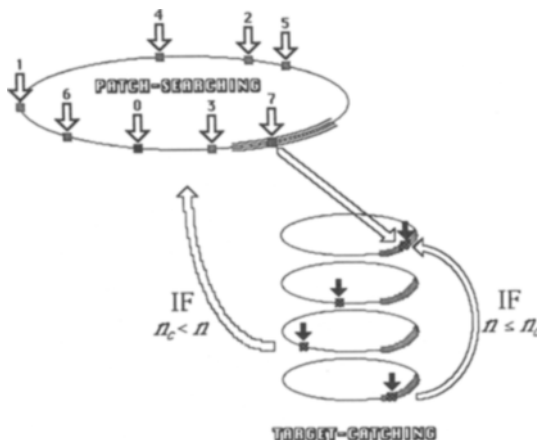

Fig. 6.   Scheme of Model 2. The patch-searching process is terminated when the searcher enters a patch region on S^1. The target-catching process is objected to a fixed-giving up step number strategy with n_c. For a more detailed explanation, see the text.

RESULT 1.5.   *At the coevolutionary goal in case of the counter-behaving target with a non-negligible body size, in order that a two-mode searching behavior is adaptable versus the targets' patchy distribution, the target size must be sufficiently small compared to the available total area per patch and each patch must contain a sufficiently small number of targets. The adopted two-mode searching has a relatively moderate change of behavior. An outstanding behavior change of two-mode searching is adaptable only when the target size is sufficiently small.*

Next, we see Fig. 5. It shows only the case when $\Delta L_0 < \sqrt{2}b$. If $\sqrt{2}b \leq \Delta L_0$, we obtain Fig. 3 again. From Fig. 3 and Fig. 5, we obtain:

RESULT 1.6.   *At the coevolutionary goal in case of the cooperative-behaving*

target, even when the target size is not negligible, if it is sufficiently small, the size effect is weak. The larger is the target size, the less adaptable is the two-mode searching behavior.

As for the adaptable two-mode searching behavior in this case, we obtain the same result as Result 1.3.

As a whole, as for the target distribution at the coevolutionary goal, we can obtain:

RESULT 1.7. *At the coevolutionary goal, the counter-behaving target takes a patchy distribution, while the cooperative-behaving target is very likely to take a uniform distribution.*

4.   Model 2

Model 2 is considered on S^1, that is, on a circle (Fig. 6). We assume that the searcher cannot distinguish the visited patch from the unvisited one. Moreover, as the found target is not assumed to be removed in Model 2, it is assumed that the searcher cannot distinguish the found target from the encountered one. Thus, the modelling space S^1 for Model 2 can be regarded as a mathematical translation of the space R^1 where patches are uniformly distributed. In each of two processes, following a discrete time, the searcher discretely changes its site on S^1 at each step. The searcher's site is selected at each step on S^1 at random independently of the previous site. The process corresponds to a Bernoulli process. The searcher is assumed to take a "fixed-giving up time (i.e., number of steps)" strategy. Note that, in Model 2, the difference between searcher's two behaviors is not practically evident. Indeed, as we shall see, these two processes are mathematically identical. Therefore, we can say that Model 2 is simply a combination of two processes with a mathematical connecting rule, while such model may be still intuitively meaningful as a metaphor. We shall see that Model 2 leads us to a particular result different from those for Model 1.

Patch-Searching Process: We consider this process on a circle of length A. On this space, there is a connected region (an arc) of length l $(< A)$, which represents the zone of patch. This situation corresponds to that when the patch (segment) of length l is uniformly distributed on R^1 with distance $\Delta S = A - l$ between the nearest-neighbor patches. Note that, as in the case of Model 1, A can be regarded as a share of space per a patch. We shall use the following notations for Model 2:

P_1^{in}:   probability of the searcher's entrance by one step into the patch. From the assumption for the process, we easily find $P_1^{in} = (l/A)(bN/l)$

$\langle n_1 \rangle$:   expected number of steps for the searcher to enter the patch,

where b can be regarded as the target size or the necessary space share per target as in Model 1, while it can be regarded as the searcher's searching capacity. It is taken into consideration that the searcher misses to find the patch even if it enters the zone of patch because the searcher arrives at a point in the gap between targets and cannot encounter the target in the zone. In mathematical terms, we introduce

the missing probability by assuming $P_1^{in} = (l/A)(bN/l)$ instead of $P_1^{in} = l/A$, then the missing probability is given by $(l - bN)/l$. With these notations, the following is easily found:

$$(2.1) \qquad \langle n_1 \rangle = \sum_{k=1}^{\infty} k \cdot P_1^{in} \left(1 - P_1^{in}\right)^{k-1} = \frac{1}{P_1^{in}}.$$

Target-Catching Process: We shall use the following notations:

P_2^{in}: probability of the searcher's catching the target in one step. From the assumption for the process, this probability is given by $P_2^{in} = b/\Delta L = bN/l$

$P_{2,k}^{in}$: probability of the searcher's catching the next target by k steps after catching a target

$P_{2,c}^{in}$: probability that after catching a target the searcher's catches the next target by a number of steps less than or equal to n_c

$\langle n_2 \rangle$: expected total number of steps in the target-catching process before the searcher gives it up

$\langle M \rangle$: expected number of targets caught in the target-catching process before the searcher gives it up.

Note that $P_1^{in} < P_2^{in}$ because $l < A$. With these notations, the following relations are found:

$$(2.2) \qquad P_{2,k}^{in} = P_2^{in} \cdot \left(1 - P_2^{in}\right)^{k-1}.$$

$$(2.3) \qquad P_{2,c}^{in} = \sum_{k=1}^{n_c} P_{2,k}^{in} = 1 - \left(1 - P_2^{in}\right)^{n_c}$$

$$(2.4) \qquad \langle M \rangle = \sum_{k=1}^{\infty} k \cdot \left(P_{2,c}^{in}\right)^{k-1} \cdot \left(1 - P_{2,c}^{in}\right) = \frac{1}{1 - P_{2,c}^{in}}.$$

Since the process is Markovian, we get:

$$(2.5) \qquad \langle n_2 \rangle = \sum_{M=1}^{\infty} \sum_{k_j=1}^{n_c} (k_1 + k_2 + \cdots + k_{M-1} + n_c) \left(\prod_{j=1}^{M-1} P_{2,k_j}^{in}\right)\left(1 - P_{2,c}^{in}\right)$$

$$= \frac{1}{P_2^{in}} \frac{1}{\left(1 - P_2^{in}\right)^{n_c}} + n_c.$$

The last equality follows by a careful but fundamental calculation of summation and by the Markovian nature of process.

Efficiency: With the above results, we shall discuss the efficiency given by:

$$(2.6) \qquad \langle E \rangle = \frac{\langle M \rangle}{\langle n_1 \rangle + \langle n_2 \rangle} = \left\{ \left(\frac{1}{P_1^{in}} + n_c\right)\left(1 - P_2^{in}\right)^{n_c} + \frac{1}{P_2^{in}} \right\}^{-1}$$

Analysis: Calculating $\partial \langle E \rangle / \partial n_c$, we obtain the following:
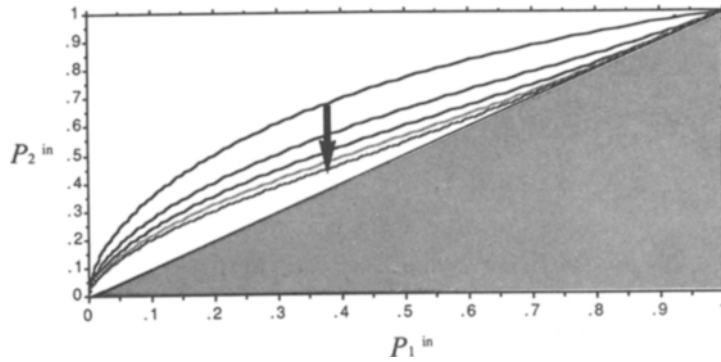
Fig. 7. $\langle E\rangle|_{n_c=n_c} < \langle E\rangle|_{\text{simple}}$ region in the P_1^{in}-P_2^{in} space. The considered region has the boundary composed of a curve and the line $P_1^{\text{in}} = P_2^{\text{in}}$. The curved boundary is given by (2.8). The considered region shrinks as n_c increases in (2.8), and vanishes at the limit $n_c \to +\infty$. The shadowed region is nonsense because $A < l$.
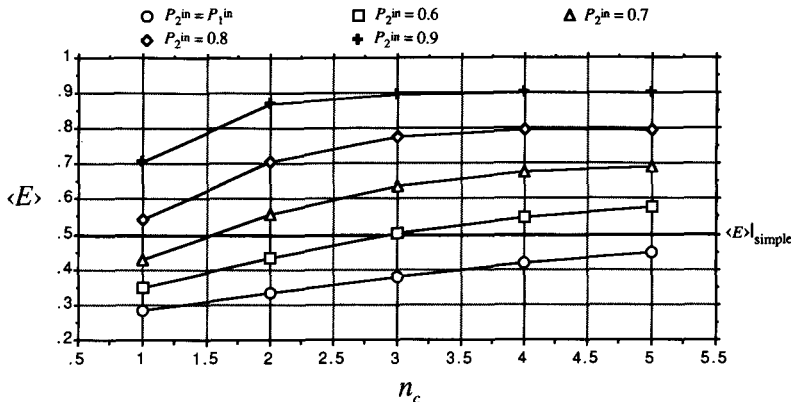

Fig. 8. n_c-$\langle E\rangle$ relation for some $P_2^{\text{in}} \cdot P_1^{\text{in}} = 0.5$. $\langle E\rangle|_{\text{simple}} = 0.5$.

LEMMA 2.1.   *For $n_c > 0$, the efficiency $\langle E\rangle$ is a monotonically increasing function of n_c.*

Thus, considering only the two-mode searching, the searcher tends to take the larger n_c. Moreover we find that the efficiency $\langle E\rangle$ is a monotonically increasing function of P_1^{in} and of P_2^{in} for $n_c \geq 1$. This is natural because both probabilities P_1^{in} and P_2^{in} express the easiness of searching.

We remark that it is beneficial for the searcher to take a simple mode searching, only when the efficiency with a simple mode searching (i.e., $n_c = 0$) is larger than that with the two-mode searching for $n_c \geq 1$. Since the simple mode searching of this model is a simple Bernoulli process, the efficiency is easily obtained as follows:

$$(2.7) \qquad\qquad \langle E\rangle|_{\text{simple}} = \frac{bN}{A} = P_1^{\text{in}}.$$

The condition $\langle E\rangle|_{n_c=n_c} < \langle E\rangle|_{\text{simple}}$ can be obtained from (2.6) and (2.7) (see Fig.

7):

$$(2.8) \qquad \frac{1 - \left(1 - P_2^{in}\right)^{n_c}}{n_c \left(1 - P_2^{in}\right)^{n_c} + 1/P_2^{in}} < P_1^{in}.$$

Now we assume a fixed finite available space A, which brings the constraint for the variable $P_1^{in} = bN/A$: For fixed b and N, $P_1^{in} = \text{const.}$ From (2.7), this means that the efficiency by the simple mode searching is constant. In Fig. 8, as n_c increases for a fixed P_1^{in}, the efficiency monotonically asymptotically reaches P_2^{in} from below. With respect to the value P_2^{in} for a fixed P_1^{in}, the lowest efficiency is realized when $P_2^{in} = P_1^{in}$, that is, $l = A$:
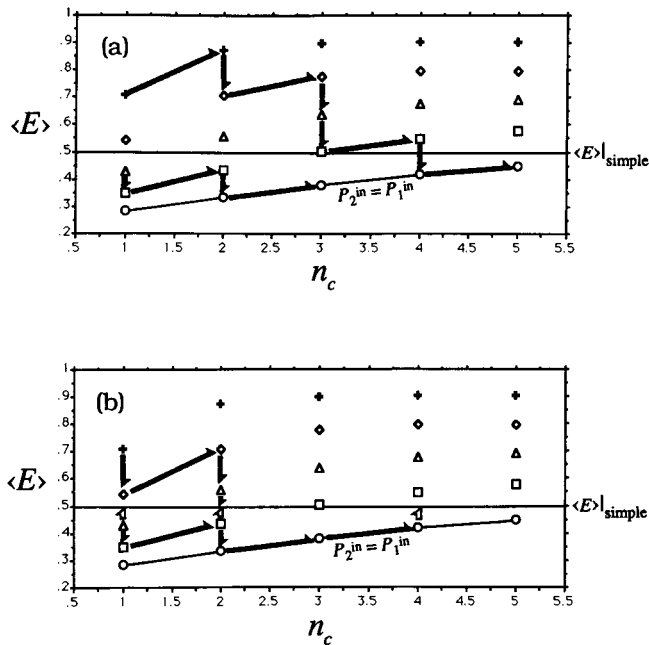

Fig. 9.   Some schematic routes of coevolutionary game in Model 2. The coevolutionary goal for the searcher is: a) two-mode searching; b) simple mode searching. The same symbol in the figure is corresponding to the same patch size. Vertical black arrows show the efficiency reduction due to a strategic expansion of target's patch size. Other black arrows show the efficiency increase due to a strategic increment of searcher's giving up step number. Vertical white arrows in (b) show the efficiency increase due to a strategic adaptation of simple mode searching, after giving up a two-mode searching.

LEMMA 2.2.   *For fixed b and N, the lowest searching efficiency is realized when $l = A$ (a uniform distribution of targets in space).*

Further, Fig. 8 shows us that:

LEMMA 2.3. *For any uniform distribution of targets, the efficiency is higher when $n_c = 0$, that is, when the searcher selects a simple mode searching, instead of any two-mode searching.*

As far as the searcher takes a two-mode searching, the counter-behaving target tends to increase its patch size. If the target continues this tendency, its distribution becomes uniform in space. Then a simple mode searching becomes the best strategy of the searcher's searching way. By this argument in case of the counter-behaving target, the coevolutionary goal is a simple mode searching versus a uniform distribution. Contrarily it is possible that the searcher takes a simple mode searching for a patchy distribution of targets at a moment in this coevolutionary game because, as the patch size is increasing, the searching efficiency can become higher for the simple mode searching than for a chosen two-mode searching (see Fig. 9b). However, note that the efficiency is independent of the patch size l when the searcher takes a simple mode searching. Thus, once the searcher takes a simple mode searching, the target's effort to reduce the efficiency by changing the patch size becomes null. Instead, reducing the total number N of targets in a patch becomes effective for this purpose. In such a case, the total number N is likely to become 1 at last. This means the targets' uniform distribution, too.

RESULT 2.1. *At the coevolutionary goal in case of the counter-behaving target, the searcher takes a simple mode searching versus the targets' uniform distribution.*

As for the case of cooperative-behaving target, Lemma 2.2 shows us that the target tends to be distributed as patchily as possible. Then as P_2^{in} becomes larger than P_1^{in}, the searcher takes a two-mode searching from Lemma 2.1. Consequently,

RESULT 2.2. *At the coevolutionary goal in case of the cooperative-behaving target, a two-mode searching behavior is adaptable versus the target distribution as patchy as possible.*

5. Discussion

Model 1: It is shown that the counter-behaving target, which tends to reduce the searching efficiency, always adopts a patchy distribution at the coevolutionary goal. In case of the cooperative-behaving target, which tends to increase the searching efficiency, a targets' uniform distribution is very likely to be adopted versus a simple mode searching behavior of searcher. Searcher's two-mode searching behavior is always adopted against the counter-behaving target, while it is adaptable against the cooperative-behaving target only when the target size and the patch size are sufficiently small and the target density is sufficiently high in the patch. Sufficiently large target size leads the searcher's behavior to a simple mode searching.

As mentioned by Knoppien and Reddingius [8], the searcher's movement on $\mathbf{R}^1$ may be regarded as an approximated projection of the movement in the higher dimensional space, that is in the real space. As for the start of target-catching process from a point middle in a patch, we can imagine as follows: In the patch-

searching process, the searcher searches a patch with *flying*. After finding a patch located two-dimensionally on a place, the searcher reaches it at a random middle point and starts to *walk* on the place in order to catch targets. Indeed, it is very likely that the patch is of 2-dimension and the searcher's searching undergoes in the 3-dimensional space. Some may feel that the target-catching process should start from a target located at the edge of patch. This is another possible assumption on the model. For example, as discussed by Hamilton [4], within a group of preys, the individuals in peripheral tend to be attacked more frequently by predators than those in the middle of the group. Note that, in this case, the patch distribution and the searcher's behavior must be of the same dimension. Also in this case, we can derive the efficiency corresponding to (1.6), substituting the following for $\langle T_2 \rangle$:

$$\langle T_2 \rangle = \frac{1}{2} \left(\frac{\Delta L}{\sigma_2} \right)^2 (M - 1) \left(M - 2 + \frac{2\Delta S}{\Delta L} \right).$$

This is a little more complex than (1.5) and brings fastidious features of mean searching efficiency. Thus, here we put aside this case as an open problem and limit our argument on Model 1, avoiding an unnecessarily too complex argument, while it may be worth being analyzed.

Model 2: The coevolutionary goal consists of a simple mode searching behavior and the counter-behaving targets' uniform distribution, or of a two-mode searching behavior and the cooperative-behaving targets' patchy distribution.

Let us incidentally consider the case when the patch size has an upper bound, say $l_{\max}$ ($< A$), due to some biological reasons: for example, since a large patch size means a low target's density in a patch, a too large patch size may lead to a too small mating efficiency among targets. Since the counter-behaving target's tendency is to expand the patch size, the patch size tends to reach $l_{\max}$. As far as $l_{\max} < A$, the searching efficiency for a two-mode searching with a sufficiently large n_c becomes higher than that for the simple mode searching (see Fig. 8). Thus, the searcher can make the searching efficiency as high as possible by a two-mode searching. At the coevolutionary goal, a two-mode searching must be chosen for the patch size $l_{\max}$. On the other hand, this upper bound has no effect on the cooperative-behaving target.

Next, let us consider another possibility that a two-mode searching may be selected by the searcher at the consequent situation in the coevolutionary game against the counter-behaving target. As far as the chosen two-mode searching has a higher searching efficiency than that gained by the simple mode searching, the searcher's behavior-switching number n_c tends to increase (Lemma 2.1). If the behavior-switching number becomes so large, is it always easy for the searcher to take a simple mode searching even at the moment when the searching efficiency becomes higher for a simple mode searching than for the previous two-mode searching? In other words, can the searcher with a large behavior-switching number be afforded to take a jumping change of strategy such as a large $n_c \to n_c = 0$? Provided that the searcher's strategy change is due to the natural selection, a mutant with a simple mode searching must appear among searchers with a two-mode

searching with a large behavior-switching number. Such a mutation may cause a too large cost, that is, may have a very small probability. In this sense, it seems to be difficult for the searcher to come to take a simple mode searching after it has adopted a two-mode searching with a large behavior-switching number. Further, as the behavior-switching number becomes larger and the patch size becomes larger, the difference between the efficiency of two-mode searching and that of simple mode searching becomes smaller (see Fig. 8). If the difference is so small that the cost of strategy change such as a large $n_c \rightarrow n_c = 0$ is larger than the gain by the change, the searcher is likely not to change its two-mode searching to a simple mode searching. By these arguments, we may say that the adaptability of a simple mode searching depends on the moment when it is adopted by the searcher in the coevolutionary game against the counter-behaving target. Even if a simple mode searching can realize a higher searching efficiency, the searcher is likely to take a two-mode searching. In this case, the two-mode searching may be regarded as an attainable final strategy, i.e., may become a coevolutionary goal for the searcher.

By Lemma 2.1, once the searcher takes a two-mode searching for a uniform distribution of counter-behaving targets, the behavior-switching step number n_c must tend to become monotonically large (see Fig. 9a). In a mathematical sense, it infinitely increases, that is, $n_c \rightarrow +\infty$. Note that, in such a limiting case, the searcher's behavior is not any two-mode searching anymore but can be regarded as a simple mode searching. This is because infinite n_c means that the searcher infinitely continues the target-searching process once it enters the process. Thus, in this case, the searcher comes to take a simple mode searching at any time, irrespectively of the previous patch-searching process. Indeed, as shown in Fig. 8, in the limit $n_c \rightarrow +\infty$, the searching efficiency asymptotically reaches that for a simple mode searching. Therefore, it is meaningless to consider the case of unrealistically large n_c. Thus, though there is no constraint on increasing n_c in Model 2, there might be a trade-off relation which defines an upper bound for increasing n_c. For example, for a prey-predator relation, since the caught prey must be removed from the patch, the patch quality decreases as the target-catching process proceeds. In this case, a too large n_c may be unfavorable for the searcher, because a large n_c means that the searcher must continue the target-catching process even after the patch quality has decreased so much that also the gain in the process has become very low. As for a host-parasite relation, a large n_c leads to a strong possibility of polyparasitism which may reduce the fitness of each juvenile laid down in the host. As a consequence, putting together biological concepts mentioned in the above arguments, we can state again that a two-mode searching may be adaptable also in Model 2.

Although Model 2 was described as a pair of one-dimensional processes, the results can be translated as those for a higher-dimensional model. Indeed, as far as only the expected values are considered in the analysis, the contents of calculation are the same, independently of the spatial dimension. For example, assuming that the expected area size of a patch is l and the expected area shared per patch is A in 2-dimensional space, we can find that the expected number of steps for the searcher to enter a patch is the same with (2.1). As for the second searching mode,

so it is.

Particularly we remark the opposite results between two models: Coevolutionary goals have the opposite tendencies. Briefly, this consequence is due to the difference of modelling structures. In Model 2, the expected number of steps for the searcher to enter a patch is independent of the patch size, so that the patch-searching process is in fact independent of the patch size. This is an important contrast between two models. Further, as far as non succeeding to catch a target, the distance from the patch or the target is nonsense for the searcher in Model 2, while it directly contributes to the probability to find the patch or the target in Model 1. The neglection of searcher's searching spatial configuration can be considered as the reason of the above-mentioned contrast. Indeed, if the searcher's present site has a probabilistic relation with the previous one in Model 2, the model shows very interesting features: the existence of optimal patch size to reduce the searching efficiency as low as possible in case of the counter-behaving target; the adaptability of two-mode searching versus such a patchy distribution. As for this modified and more complex (thus, partially computer-aided) model, we will report in another article. At last, we can say that the advantage of patchy distribution to reduce the searching efficiency, which has been discussed by Cain [1] and other computer-simulated works, may be really the matter of spatially heterogeneous structures.

We have assumed that the target distribution strategy is restricted by (H), which is a linear relation between the patch size and the distance between nearest-neighbor patches. However, this linearity is of course not necessary. Indeed, it may be possible to consider another non-linear type of relation between them. Then, results change quantitatively, but it can still be shown by a similar argument that a two-mode searching is adaptable as a coevolutionary goal.

In our models, the inside and the outside of a patch are assumed to be rigorously distinguished. This assumption has been explicitly or implicitly introduced also in the previous models, in which the possibility that the searcher may go out of the patch in the target-catching process has been systematically neglected. In some cases, such a possibility may have a significant effect on the considered searching efficiency. Knoppien and Reddingius [8] focused on this point and analyzed a model which includes an ambiguous patch boundary, that is a boundary such that the inside and the outside of a patch are not necessarily distinguished. In some cases, such a model may be more realistic with respect to the concept "patch". But in other cases, it seems that a model with a clear boundary of patch may be adaptable: For example, in the case of the relation between a leaf-miner and its parasitoid (Kato [6], [7]), a leaf can be regarded as a patch. Further, also in the case of the relation between a crowd of eggs and the predator, the boundary of egg-patch may be easily distinguished since eggs are gregariously laid, for example, as those jellied by a frog, or as those arranged densely by an insect. While there is a variety of biological definitions of the concept "patch" (Wiens [18]), it may be necessary to make clear which factor of real nature is neglected or emphasized by the introduced mathematical patch structure.

Undoubtedly our models are too simple to be compared directly with real

phenomena. But, as far as similar mathematical models are concerned, any more realistic assumption has the drawback of leading to a much more difficult mathematical analysis. It appears that any more realistic model is suitable for computer simulation rather than for analytical investigation. We believe that, to consider the real phenomena or the sophisticated models, it should be worth while knowing what results are brought from those simplified models in which only a few factors are picked up and others are neglected or averaged up into parameters. It is expected that, as metaphors, our models will give some intuitive contributions to consider the real phenomena and to compose and analyze other sophisticated models.

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