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Coevolutionary Game Modelling Consideration on The Relation Between the Optimalities of Two-mode Searching Behavior and the Target's Patchy Distribution

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二相探索形式の最適性と目標のパッチ状分布との関係についての共進化ゲームモデル

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ABSTRACT

We 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. Four intuitive models are presented: Model 1 constructed by a Wiener process on $\mathbb{R}^1$; Model 2 by a time-discrete Markov process on $\mathbb{S}^1$, that is, on a circle; Model 3 by a time-discrete stochastic process on $\mathbb{S}^1$. In Model 3, differently from Model 2, the searcher's present location is assumed to be influenced by the past passage configuration. Model 4 is different from the others, applied the fractal concept for the trajectory pattern made by the target. The optimality of the trajectory pattern against the searcher is analyzed. These different models give a variety of 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.

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.[1), 2), 6), 7), 8), 9), 10)]

In this paper, we mathematically demonstrate that a two-mode searching is possible to 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.[11)] If the distribution is assumed to be directed to make the mean efficiency as high as possible, this game can be regarded cooperative. We call the former type of target "the counter-behaving target" and the latter "the cooperative-behaving target".

We deal with three models: Model 1 constructed by a Wiener process; Model 2 by a time-discrete Markov process; Model 3 by a time-discrete stochastic process. Model 3 can be regarded as a modification of Model 2 of the quoted paper. The searcher's present location is assumed to be influenced by the past passage configuration, which is an essentially different assumption from that for Model 2. Model 4 is different from the others, applied the fractal concept for the trajectory pattern made by the target. The optimality of the trajectory pattern against the searcher is analyzed.

MODELLING ASSUMPTIONS

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 $N\Delta L = l$.

We 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:

$$\Delta S + N\Delta L = A, \tag{H}$$

where A can be regarded as a share of space per patch. The target must select its distribution pattern under this restriction.

We 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: patch-searching process and target-catching process. 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 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).

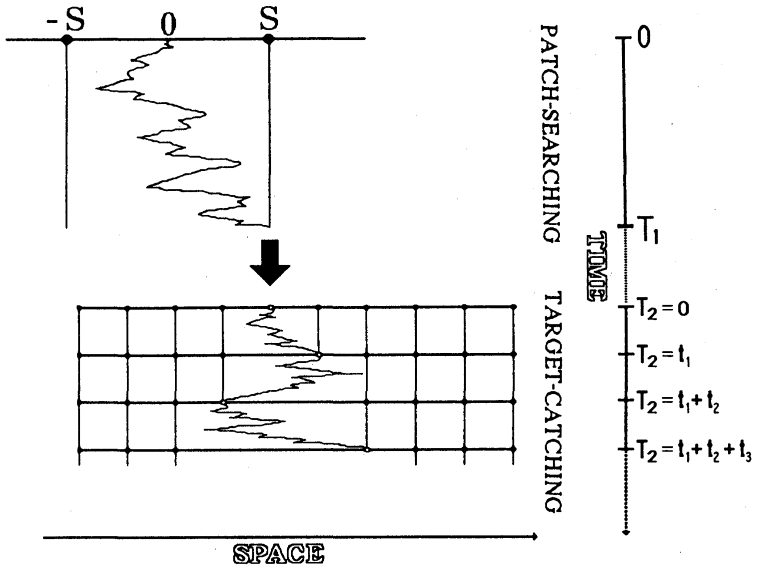

Fig. 1. Scheme of Model 1. For explanation, see the text.

MODEL 1

Model 1 is considered on a one-dimensional space $\mathbb{R}^1$ (Fig. 1). In each of two processes, the searcher is assumed to be a point moving continuously on $\mathbb{R}^1$ as a Wiener process, that is as a Brownian motion. Moreover, we assume that there is no drift, which means that the searcher moves completely at random without any biased direction. As shown in Fig. 1, the patch-searching process is terminated when the searcher encounters a point on $\mathbb{R}^1$. 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. 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.

Patch-Searching Process: For this process, we assume the Wiener process with infinitesimal variance $\sigma_1{}^2$. The searcher is assumed to begin its search at the origin on $\mathbb{R}^1$ (Fig. 1). Two points are set at $x = -S$ and $x = S$ as nearest-neighbor two patches. Thus, $\Delta S = 2S$. 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), from which we can obtain the mean time $\langle T_1 \rangle$ [9]:

$$\langle T_1 \rangle = \left(\frac{\Delta S}{2\sigma_1} \right)^2 . \tag{1.1}$$

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).

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), which gives the mean time $\langle t_j \rangle$ [9]:

$$\langle t_j \rangle = j \left(\frac{\Delta L}{\sigma_2} \right)^2 . \tag{1.2}$$

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

$$\langle T_2 \rangle = \left\langle \sum_{j=1}^{M-1} t_j \right\rangle = \sum_{j=1}^{M-1} \langle t_j \rangle = \frac{1}{2} \left(\frac{\Delta L}{\sigma_2} \right)^2 M(M-1) . \tag{1.3}$$

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

$$\langle E \rangle_M = \frac{M}{\langle T_1 \rangle + \langle T_2 \rangle} = \frac{M}{\frac{1}{4}\left(\frac{\Delta S}{\sigma_1} \right)^2 + \frac{1}{2}\left(\frac{\Delta L}{\sigma_2} \right)^2 M(M-1)} . \tag{1.4}$$

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

$$M^* = \frac{1}{\sqrt{2}} \frac{\Delta S}{\Delta L} \frac{\sigma_2}{\sigma_1}. \tag{1.5}$$

When $M = M^*$, the efficiency becomes

$$\langle E \rangle_{M^*} = \sqrt{2} \left\{ \frac{\Delta L}{\sigma_2} \left(\frac{\Delta S}{\sigma_1} - \frac{1}{\sqrt{2}} \frac{\Delta L}{\sigma_2} \right) \right\}^{-1} . \tag{1.6}$$

Seno (1991) analyzed (1.6) and showed the followings [9]: 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.

MODEL 2

Model 2 is considered on $\mathbb{S}^1$, that is, on a circle (Fig. 2). 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 $\mathbb{S}^1$ for Model 2 can be regarded as a mathematical translation of the space $\mathbb{R}^1$ where patches are uniformly distributed. In each of two processes, following a discrete time, the searcher discretely changes its site on $\mathbb{S}^1$ at each step. The searcher's site is selected at each step on $\mathbb{S}^1$ at random independently of the previous site. The searcher is assumed to take a "fixed-giving up time (i.e., number of steps)" strategy.

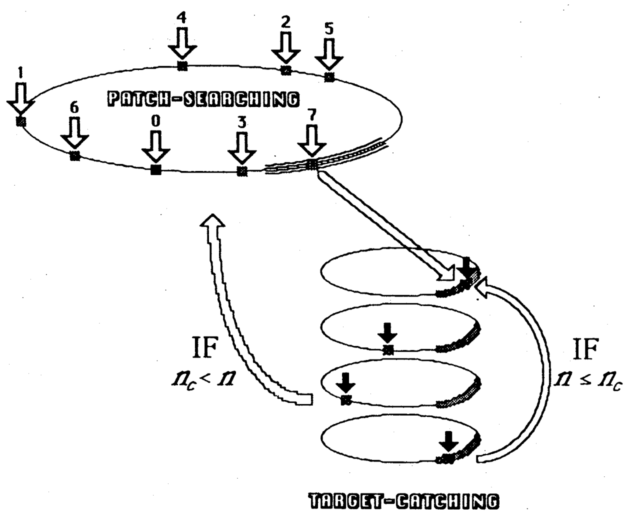

Fig. 2. Scheme of Model 2. For explanation, see the text.

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 $\mathbb{R}^1$ 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 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 $P_1^{\text{in}} = (l/A)(bN/l)$

$\langle n_1 \rangle$: 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. With these notations, the following is easily found [9]:

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

Target-Catching Process: We 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 $P_2^{\mathrm{in}} = b/\Delta L = bN/l$.

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

$P_{2,c}^{\mathrm{in}}$: 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.

With these notations, the followings are found [9]:

$$\langle M \rangle = \sum_{k=1}^{\infty} k \cdot \left(P_{2,c}^{\mathrm{in}}\right)^{k-1} \cdot \left(1 - P_{2,c}^{\mathrm{in}}\right) = \frac{1}{1 - P_{2,c}^{\mathrm{in}}} . \tag{2.2}$$

$$\langle n_2 \rangle = \sum_{M=1}^{\infty} \sum_{k_j=1}^{n_c} (k_1 + k_2 + \cdots + k_{M-1} + n_c) \left(\prod_{j=1}^{M-1} P_{2,k_j}^{\mathrm{in}} \right) \left(1 - P_{2,c}^{\mathrm{in}}\right) \tag{2.3}$$

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

Efficiency: With the above results, the efficiency is given by

$$\langle E \rangle = \frac{\langle M \rangle}{\langle n_1 \rangle + \langle n_2 \rangle} = \left\{ \left(\frac{1}{P_1^{\mathrm{in}}} + n_c \right) \left(1 - P_2^{\mathrm{in}}\right)^{n_c} + \frac{1}{P_2^{\mathrm{in}}} \right\}^{-1} . \tag{2.4}$$

Analysis: 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:

$$\langle E \rangle|_{\mathrm{simple}} = \frac{bN}{A} = P_1^{\mathrm{in}} . \tag{2.5}$$

The condition $\langle E \rangle|_{n_c = n_c} < \langle E \rangle|_{\mathrm{simple}}$ can be obtained from (2.4) and (2.5):

$$\frac{1 - \left(1 - P_2^{\mathrm{in}}\right)^{n_c}}{n_c\left(1 - P_2^{\mathrm{in}}\right)^{n_c} + 1 / P_2^{\mathrm{in}}} < P_1^{\mathrm{in}} . \tag{2.6}$$

Consequently from the analysis on (2.6), Seno (1991) shows that 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.[9] With some additional conditions, Seno (1991) consider such 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, too.[9]

MODEL 3

This is the model modified from Model 2 (Fig. 3). Differently from Model 2, the distance between a site and the following site is assumed to be an exponential random variable. The direction of each step is selected at random, that is, with the probability 1/2 the searcher jumps to the next site in the clockwise or in the anti clockwise direction.

Patch-Searching Process: At first, we must select the initial site x_0 of the searcher out of the patch. It is assumed that the initial site is uniformly distributed out of the patch. The next searcher's step is subjected to the exponential distribution with expected value λ_1, that is, with probability density function given by:

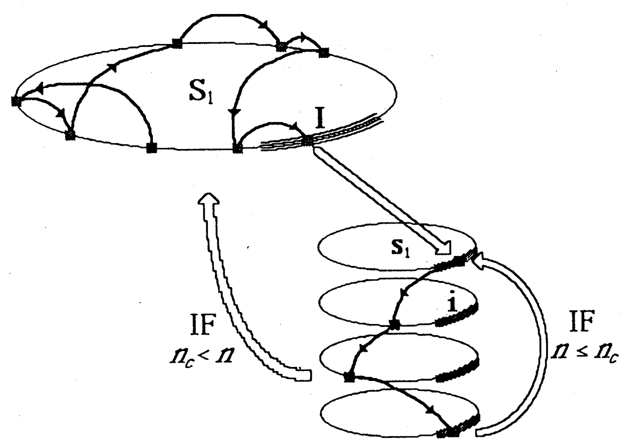

Fig. 3. Scheme of Model 3. For explanation, see the text.

$$f_1(\Delta x) = \frac{1}{\lambda_1}\exp\left(-\frac{\Delta x}{\lambda_1}\right). \tag{3.1}$$

For the patch-searching process, we use the following notations:

$x \in \mathbf{S}_1 \equiv [0, A] \bmod A$

I: zone of patch, $\mathbf{S}_1 \supset \mathbf{I} \equiv (A - l, A) \bmod A$

G: zone out of patch, $\mathbf{S}_1 \supset \mathbf{G} = \mathbf{S}_1 - \mathbf{I} \equiv [0, A - l] \bmod A$

$P^n{}_{\mathbf{x}}(x_0)$: probability of the searcher's entrance by n steps into the patch from the initial point x_0 out of the patch with a configuration $\mathbf{x} \equiv (x_0, x_1, ..., x_{n-1})$ in **G**, independently of the point reached in the patch

$\langle n_1 \rangle$: expected number of steps for the searcher to enter firstly the patch, averaged with respect to the initial point and the configuration of searching.

With these notations, through the relation (3.2), Seno and Buonocore (1991) obtains [10]

$$\langle n_1 \rangle = \sum_{n=1}^{+\infty} \int_G dx_0 \int_G dx_1 \int_G dx_2 \cdots \int_G dx_{n-1} n \cdot P^n{}_x(x_0). \tag{3.2}$$

$$P^n{}_x(x_0) = \left(\frac{1}{2\lambda_1}\right)^{n-1} \left\{\mathrm{sech}\left(\frac{A}{2\lambda_1}\right)\right\}^n \sinh\left(\frac{l}{2\lambda_1}\right) \cosh\left(\frac{2x_{n-1} - A + l}{2\lambda_1}\right) \prod_{k=0}^{n-2} \cosh\left(\frac{A - 2|x_k - x_{k+1}|}{2\lambda_1}\right). \tag{3.3}$$

Target-Catching Process: The searcher's initial site in the target-catching process is the center of target's region which has length $2b$ (see Fig. 3). Now we regard the center point of target's region as the origin on $\mathbb{S}^1$. Further, after catching a target, the searcher is assumed to begin always its next target-catching process from the center of target's region. The searcher's step is subjected to the exponential distribution with expected value λ_2, that is, with probability density function:

$$f_2(\Delta x) = \frac{1}{\lambda_2} \exp\left(-\frac{\Delta x}{\lambda_2}\right). \tag{3.4}$$

The searcher is assumed to take a fixed-giving up step strategy. In nature, the searcher may stochastically go out of the patch, and the smaller the patch size is, the larger such probability must be.

Below we list up the notations for the target-catching process:

$z \in \mathrm{s}_1 \equiv [0, \Delta L] \bmod \Delta L$

i:	target's region, $\mathrm{s}_1 \supset \mathrm{i} = \mathrm{i}_1 \cup \mathrm{i}_2 \equiv [0, b) \cup (\Delta L - b, \Delta L) \bmod \Delta L$
g:	region out of target, $\mathrm{s}_1 \supset \mathrm{g} = \mathrm{s}_1 - \mathrm{i} \equiv [b, \Delta L - b] \bmod \Delta L$
n_c:	fixed-giving up step, i.e., the behavior-switching step number in the target-catching process
$P^n{}_{\mathbf{z}}$:	probability of the searcher's catching the target by n steps with a configuration $\mathbf{z} \equiv (z_0, z_1, \ldots, z_{n-1})$ in g
$P^c{}_{\langle \mathbf{z} \rangle}$:	probability of the searcher's catching a target by less than n_c steps, averaged with respect to the configuration of searching

$\langle n_2 \le n_c \rangle$: expected number of steps for the searcher to catch another target after catching one, averaged with respect to the configuration of searching, conditional on the number of steps being equal to or less than the fixed-giving up step number 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.

With these notations, the following relations are found [10]:

$$\langle M \rangle = \frac{1}{1 - P^c_{(l)}} \tag{3.5}$$

$$\langle n_2 \rangle = \{\langle M \rangle - 1\} \langle n_2 \le n_c \rangle + n_c \, . \tag{3.6}$$

$$P^n_z = 2\left(\frac{1}{2\lambda_2}\right)^n \left\{\mathrm{sech}\left(\frac{d}{2\lambda_2}\right)\right\}^n \sinh\left(\frac{r}{\lambda_2}\right) \cosh\left(\frac{d-2z_1}{2\lambda_2}\right) \cosh\left(\frac{d-2z_{n-1}}{2\lambda_2}\right) \prod_{k=1}^{n-2} \cosh\left(\frac{d-2|z_{k+1}-z_k|}{2\lambda_2}\right). \tag{3.7}$$

Efficiency: With the above results, the mean efficiency is given by

$$\langle E \rangle = \frac{\langle M \rangle}{\langle n_1 \rangle + \langle n_2 \rangle}. \tag{3.8}$$

Analysis: Made use of tiresome numerical calculations, the results obtained by Seno and Buonocore (1991) [10] are the followings: If there is no constraint on the distribution, the counter-behaving target takes l^* ($< A$) as its patch size at the goal of coevolutionary game with the searcher's searching behavior, while the cooperative-behaving target takes a dense patchy distribution (every nearest-neighbor targets touch each other in each patch) or a uniform distribution. If there is a constraint for the patch size l: $l_{min} \le l \le l_{max}$, and $l_{min} \le l^* < l_{max}$, then the counter-behaving target can take l^* as its patch size at the goal of coevolutionary game, while the cooperative-behaving target takes l_{min} or l_{max} at the goal. However, especially in case of the counter-behaving target, if $l^* < l_{min}$, the coevolutionary game leads the patch size to l_{min}. If $l_{max} < l^*$, the game leads the patch size to l_{max}. In this case, a simple model searching can become a coevolutionary goal for the searcher against the counter-behaving target.

MODEL 4

Model 4 considers a specific situation, differently from three models presented above. Only one target is considered, which makes a trajectory in the 2-dimensional space for the searching process (Fig. 4). The trajectory corresponds to the patch considered for the other models. The searcher's patch-searching process is assumed to encounter the trajectory. After the encounter, by tracing the trajectory the searcher is assumed to search the target. This corresponds to the target-catching process. This type of searching behavior is observed for the predator against some leaf-miner.[3), 4)]

The target's trajectory is assumed to expand the diameter l, which is defined as the minimal diameter of the disc that can cover the whole trajectory. The total length of the trajectory is assumed to be J.

The expected time T_1 for the searcher to encounter the trajectory in the patch-searching process is assumed to be inversely proportional to the area expanded by the trajectory, l^2. On the other hand, the expected time T_2 for the searcher to find the target in the target-catching process is assumed to be proportional to the total length of the trajectory, J. The above argument gives the probability for the searcher to catch the target per unit time:

$$p \propto l^2 + \frac{\gamma}{J}, \qquad (4.1)$$

where γ is a positive constant. The expected searching efficiency is corresponding to $1/p$.

We consider the approximation for the target's fractal trajectory by a number of line segments with the length w. Then, the required number m of segments is approximately given by J/w.

Following Katz and George (1985) [5)],

$$l \propto m^{(1-D)/D} \cdot J \qquad (1 \leq D \leq 2), \qquad (4.2)$$

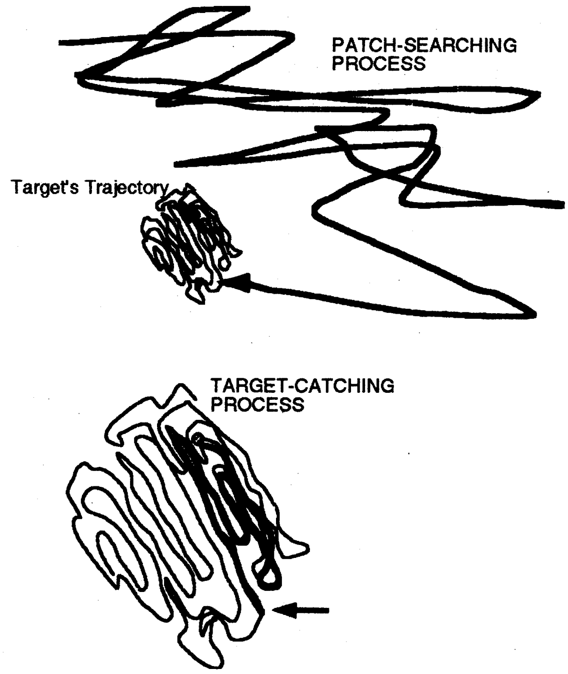

Fig. 4. Scheme of Model 4. For detail explanation, see the text.

where D is the fractal dimension to characterize the spatial pattern of the trajectory. Assume that the segment length w is characterized by the mechanism for the target to make the trajectory. Thus, w is assumed to be determined, for example, by the relation between the physiology of target organism and the structure of space. In this sense, the trajectory constructed by a number of line segments with the length w can realize the essential nature of the trajectory. Now, made use of the relations (4.1) and (4.2), the catching probability p is expressed as

$$p = \alpha J^2 m^{2(1-D)/D} + \frac{\beta}{J}, \tag{4.3}$$

where α and β are positive constants. Analyzed $\partial p/\partial J$, p takes the minimal value when $J = J^*$:

$$J^* = \left(\frac{\beta}{2\alpha}\right)^{1/3} m^{2(D-1)/3D}. \tag{4.4}$$

This J^* can be regarded as the optimal strategy for the target to reduce the searching efficiency as low as possible. If m can be considered as the time length for the target to make the trajectory, the existence of the optimum J^* means that the optimal time length to make the trajectory exists. In case of the prey-predator relation, the length may be determined with some additional conditions for the prey's survival or reproduction.

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