Exploration of Optimal Giving-up Time in Uncertain Environment: a Sit-and-wait Forager

Kinya Nishimura*

Faculty of Fisheries, Hokkaido University, Hakodate 041-8611, Japan

I address variability of giving-up time of a sit-and-wait forager in a stochastic environment. Behavioral variability is considered as an essential unavoidable feature of animals. In a stochastic environment, this unavoidable behavioral variability will increase. Thus, the existence of some behavioral variation would be considered to be a constraint. I analyse the expected long-term reward rate for a model of patch exploitation by a sit-and-wait forager as a function of giving-up time (GUT) given environmental stochasticity and a base behavioral variability. While the animal is learning about the environment, a mixed strategy is favored and thus, more variability is added to behavior. I claim that it is important to study not only the final optimal strategy but also the strategy used during the exploration process.

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Introduction

Most behavioral and morphological characters have been designed by natural selection in the course of evolution. Foraging behavior is one of the most important components of the Darwinian fitness of animals and is believed to be a target of natural selection. Optimization is a heuristic approach to understand how natural selection acts on characters like foraging behavior (Stephens & Krebs, 1986). Many factors may constrain optimization in natural selection (Maynard Smith, 1978). In "foraging theory" several constraints have been considered in order to evaluate optimal performance of forager (reviewed in Stephens & Krebs, 1986).

Patch exploitation has been one of the main topics in foraging study. Patch residence time has been tackled as an optimality problem for various environmental situations (Charnov, 1976;

Cuthill *et al.*, 1990; Green, 1984; Green & Nunez, 1986; Iwasa *et al.*, 1981; Kacelnik *et al.*, 1990; McNamara & Houstion, 1985, Orians & Pearson, 1979).

Studies of patch exploitation can be categorized into single-prey loader and multiple-prey loader problems (Orians & Pearson, 1979). In the most idealized case of the multiple-prey loader problem, a forager exploits a patch with continuous increasing but decelerating reward function with respect to exploitation time (Charnov, 1976). On the other hand, for single-prey loader, the reward function in a patch has an on-off form (Green & Nunez, 1986; Nishimura, 1992).

In several patch exploitation situations, a single-prey loader cannot know whether a patch contains a prey. For a sit-and-wait predator attacking prey that hide, prey availability in a patch is not apparent at the time of entering the patch. Prey size is also often uncertain until the hunter actually catches an item (Nishimura, 1988; Nishimura & Abe, 1988). Patches would often be

* E-mail: kinya@fish.hokudai.ac.jp.

indistinguishable for that type of forager. If all patches contain prey and patches can be thought of as identical, the single-prey loader should stay in each patch until it gets prey. Giving up before getting a prey wastes the time spent in the patch (Iwasa et al., 1981).

However, if the indistinguishable patches are different in their quality, particularly in prey existence or prey encounter rate, a forager should adopt a policy; leave as soon as it gets a prey or after a certain duration without finding prey (Green & Nunez, 1986; McNamara & Houstion, 1985; Nishimura, 1991, 1992). Green & Nunez (1986) and Nishimura (1991, 1992) analysed optimal time waiting for a prey in patch (giving-up time, GUT) for a predator taking only one prey in a stochastic environment in which prey encounter rates vary among patches.

Sometimes, behavioral performance shows variability (Houston & McNamara, 1985; Kacelnik et al., 1990; Kamil et al., 1993; Nishimura, 1988; Nishimura & Abe, 1988). Several psychologists and behavioral ecologists have studied behavioral variability (Gibbon, 1977; Gibbon et al., 1988; Kacelnik et al., 1990). Psychologists found that variability of a behavioral performance follows a scalar property, with the coefficient of variation being constant (Kacelnik et al., 1990). This implies a mechanism connecting performance and reference memory (Kacelnik et al., 1990). The psychological argument asserts that behavioral variability is constrained in such a way that mean and variance have a particular relationship under a given condition.

Other than some intrinsic behavioral variability that cannot be eliminated, behavioral variability should be related to the nature of environmental uncertainty for the animal. When a predator makes decisions (patch choice and patch residence time), it cannot have much knowledge about what will happen and, thus, it faces an uncertain situation. Elimination of this uncertainty is not easy.

When the forager has little knowledge about the environment, it may search for an appropriate decision by trying a series of decisions. Therefore, the variability of decisions may be large in an uncertain environment and small when there is little uncertainty, but never declines to zero. Behavioral variability would reflect how the forager evaluates environmental uncertainty. When the forager explores the environmental state, behavioral variability is large. After some foraging trials, the forager would somewhat know the environmental state, similar to a statistician knowing parameters of a random event after several sampling. Thus, the variability might decline to a certain level when the knowledge about the environment attains a stationary state.

The variable response to the external state is often considered a constraint (Yoshimura & Shields, 1987, 1995). Another explanation of behavioral variability is that it is sometimes considered as a mixed optimal strategy of organisms (Caraco, 1980; Levins, 1968; León, 1991; Real & Ellner, 1992; Sasaki & Ellner, 1995; Schaffer, 1974). Therefore, phenotypic variability should be evaluated in aspects of constraint and strategy.

I consider a patch exploitation process of a sit-and-wait prey hunter that takes at most one prey in each visit at a patch. The hunter always experiences environmental uncertainty, particularly, when it moves into a new habitat. My interest is the decision on patch leaving time. Once it enters a patch, the forager might leave as soon as it gets a prey or give up after a certain time without finding a prey (giving-up-time; GUT). I consider the process by which the forager searches the optimal GUT. In the exploration process, the forager finds a good way of exploiting patches, and finally attains the optimal strategy.

I consider the exploration process of optimal GUT in a stochastic environment. Figure 1 shows a hypothesized process of behavioral mechanism. The base behavioral variability is given as a constraint. While seeking optimal GUT, the forager changes mean GUT. In the transient process, I evaluate whether strategic behavioral variance added to the base behavioral variance maximises the reward, and environmental uncertainty and the basic behavioral variability would affect the transient strategy of behavioral decision.

The optimal strategy that should finally be adopted by the forager has been analysed by the previous studies (e.g. Green & Nunez, 1986; Nishimura, 1991, 1992). My special concern is what would occur in strategy of GUT during searching the optimal solution. Although evaluation of final optimal solution is the important
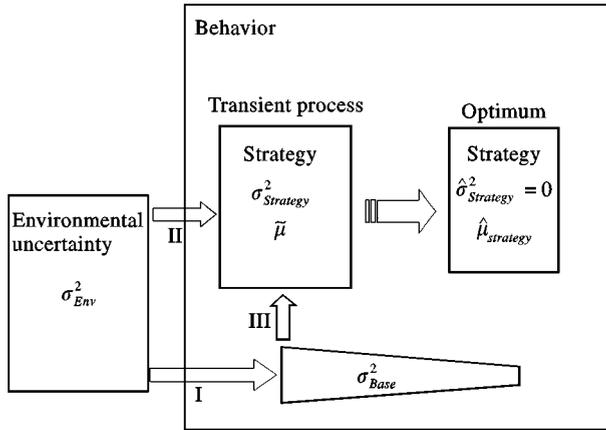
FIG. 1. The mechanisms that generate and degenerate behavioral variability. I: the base behavioral variability is generated by environmental uncertainty (particularly, when the uncertainty is changing). II: environmental uncertainty affects strategic behavior (decision of GUT). III: base behavioral variability also affects strategic behavior. In transient process (seeking for the globally optimal strategy), strategic decision changes. In the process, conditional optimal distribution of GUT strategy is determined by variance ($\sigma^2_{Strategy}$) given a mean GUT($\tilde{\mu}$). Mean GUT would shift to the optimum. In final state strategic component of behavioral variability is degenerate to zero ($\hat{\sigma}^2_{Strategy} = 0$) and GUT is a certain single finite time, $\hat{\mu}_{Strategy}$. During the transient process, the base behavioral variability may or may not decrease.

issue for evolutionary biology, if unstationary stochastic process is a reality of the nature, optimization in a transient process is also an important issue. I construct a patch exploitation model of a sit-and-wait forager incorporating environmental stochasticity and base behavioral variability, and evaluate how behavioral variability would be by the strategy of the forager, when it seeks the optimal strategy.

I do not explicitly track the information acquisition process in which base behavioral variability is changed. Therefore, the generation and/or reduction of base behavioral variability is not mechanistically tracked. However, I implicitly hypothesize that behavioral variability would be caused partially by information ambiguity, and the forager should adjust a strategic decision given an environmental uncertainty and the base behavioral variability while seeking the optimal strategy.

The Model

Here, I present a scenario in which the forager is faced with a patch exploitation problem. There

are many patches in the environment. Assume that the patches are identical in appearance, and the forager visits patches randomly. The forager takes at the most one prey during each visit to a patch. Within patches, prey encounters occur as a Poisson process that is assigned an instantaneous prey encounter rate parameter, λ. The instantaneous prey-encounter rate varies randomly in every visit of patches. The forager makes a decision (determines a GUT) at the time of entering the patch.

UNCONSTRAINED FORAGER

If the forager tends to act in a way that would maximize fitness, without being constrained, to show some behavioral variability, and if it can immediately find an optimal solution, then it adopts a single GUT in a visiting patch. Setting a GUT before entering a patch is advantageous if the forager cannot obtain any useful information to estimate patch quality during the stay in the patch. Assuming that the forager is a rate maximizer, then the long-term expected reward rate by adopting a unique GUT, T_g is expressed by

$$G(T_g) = \frac{\int_0^\infty \zeta(\lambda)(1 - e^{-\lambda T_g})d\lambda - c\tau}{\tau + \int_0^\infty \zeta(\lambda)\frac{1}{\lambda}(1 - e^{-\lambda T_g})d\lambda}, \quad (1)$$

(see Nishimura, 1991), where $\zeta(\lambda)$ is a probability density function of prey encounter rate generating environmental stochasticity, τ the average travelling time between patches and c the travelling cost per unit time relative to the searching cost per unit time. When there is a great uncertainty about patch quality, that is, when the variance of prey-encounter rate among patches is large [large variance of $\zeta(\lambda)$], the GUT should be a finite time (Green & Nunez, 1986; McNamara & Houstion, 1985; Nishimura, 1991, 1992).

CONSTRAINED FORAGER: VARIABLE GUT

Now, let us consider that the performance of the forager must be variable. Variability of behavior can often be induced by stochasticity of the environment and it changes with level of

ambiguity about the environment. Phenotypic or behavioral random variability often decreases fitness at the optimum (Yoshimura & Shields, 1987, 1995), but in other cases the random variability increases fitness (Levins, 1968; Sasaki & Ellner, 1995).

Here, I survey whether the forager should adopt a single strategy or a mixed strategy while seeking the optimal GUT. The problem is basically formalized by the following elements: (1) environmental stochasticity that is characterized by a probability function of prey encounter rate in each patch and (2) intrinsic behavioral variability. Supposing the forager chooses a GUT, the actual behavioral performance exhibits the base intrinsic variability around the GUT.

To survey how the forager should behave in the discovering process of the optimal GUT, I consider a simple example of stochasticity of the instantaneous prey encounter rate λ. I assume that the instantaneous prey encounter rate changes between two values randomly, λ_1 and λ_2, with probabilities p_1 and p_2 ($p_1 + p_2 = 1$, $\lambda_1 < \lambda_2$). Such a simple example of stochasticity of instantaneous prey encounter rate can mimic a natural stochastic environment in which some patches are bad (rate $= \lambda_1$) and some are good (rate $= \lambda_2$).

I represent the base behavioral variability by assuming that the giving-up-time has a Gamma distribution, $g(t|\mu, \sigma_{Base}^2)$, with a strategic mean (μ), and the base variance (σ_{Base}^2), and the total behavioral variability follows with a compound distribution of gammas with a strategic distribution, $\rho(t|p(\mu), \sigma_{Base}^2) = g(t|\mu, \sigma_{Base}^2)\ p(\mu)$, where $p(\mu)$ is a probability distribution of strategy. Given that the variance of $p(\mu)$ is $\sigma_{Strategy}^2$, the total behavioral variability is $\sigma_{Total}^2 = \sigma_{Base}^2 + \sigma_{Strategy}^2$ (see the appendix). If $p(\mu)$ is a Dirac delta function, it means that the forager adopts a single GUT strategy, and $\sigma_{Strategy}^2$ vanishes.

The expected reward rate given that the forager adopts a distribution of GUTs strategy, $p(\mu)$, is

$$G(p(\mu)) = \frac{p_1 E_t[\Psi_1(t)] + p_2 E_t[\Psi_2(t)] - c\tau}{\tau + p_1 E_t[\Phi_1(t)] + p_2 E_t[\Phi_2(t)]},$$

$$(i = 1, 2), \qquad (2)$$

where $\Psi_i(t) = 1 - e^{-\lambda_i t}$ is the expected probability to get a prey and $\Phi_i(t) = (1/\lambda)(1 - e^{-\lambda_i t})$ is the expected waiting time when using a GUT $= t$ in i-th patch and the expectations are the weighted means of probability function, $\rho(t|p(\mu), \sigma_{Base}^2)$.

Notice that the fitness criterion, $G(p(\mu))$ (the division of the expectation of gain by the expectation of time) is conventional one that is used in study of foraging theory (Stephens and Krebs, 1986; Templeton and Lawlor, 1981), and different from the criteria used in study of life-history evolution (Levins, 1968; Sasaki & Ellner, 1995).

Now consider $p(\mu)$. If a mixed strategy is used, $p(\mu)$ has a non-zero variance, and if a single strategy is used, $p(\mu)$ has no variance. To tackle this problem I assume a simple strategy that includes single strategy and mixed strategy:

$$p(\mu) = \begin{cases} p(\mu_1) = 0.5, \\ p(\mu_2) = 0.5. \end{cases}$$

The strategic variance is $\sigma_{Strategy}^2 = \frac{1}{4}(\mu_1 - \mu_2)^2$. or a given mixed strategy, the variance, $\sigma_{Strategy}^2$, would vanish when the forager adopts $\mu_1 = \mu_2$.

I conduct a numerical analysis of the expected reward rate with parameter set: $c = 0.05$, $\tau = 0.1$, $\lambda_1 = 0.01$, $\lambda_2 = 10$, $p_1 = 0.1$ and $p_2 = 0.9$. Figure 2 shows the reward rate to strategic GUTs (μ_1 or μ_2) given that the forager adopts mean GUT ($\tilde{\mu} = 4$). An unconstrained forager ($\sigma_{Base}^2 = 0$) should adopt a mixed strategy with larger variance than constrained forager's (see Fig. 2). While seeking the optimal GUT, the forager may choose long or short mean GUT. Figure 3 shows the total behavioral variance and the expected reward rate, when the forager adopts conditional optimization with strategic mean GUT. When the forager begins to search optimum beginning with a long GUT, a mixed strategy with large variance is favorable. The strategic variability is smaller when the base behavioral variability is large than when the base behavioral variability is small. On the contrary, when the forager begins to search optimal beginning with a short GUT, a single strategy is favorable regardless of the magnitude of base behavioral variability.

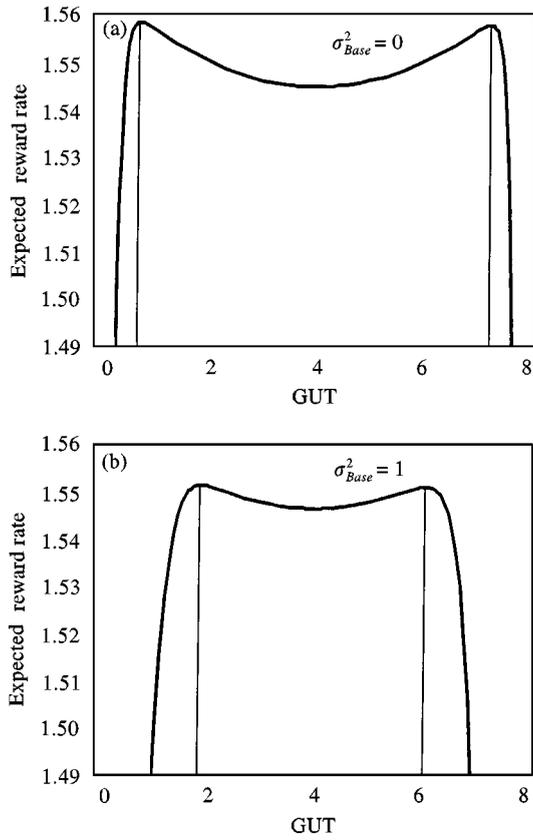After exploring, the forager will find the optimal GUT in a given condition. In an optimal

FIG. 2. The mixed strategy of GUT given that the mean GUT is 4-unit time. Solid spikes exhibit optimal mixing of GUTs in each level of base behavioral variability.
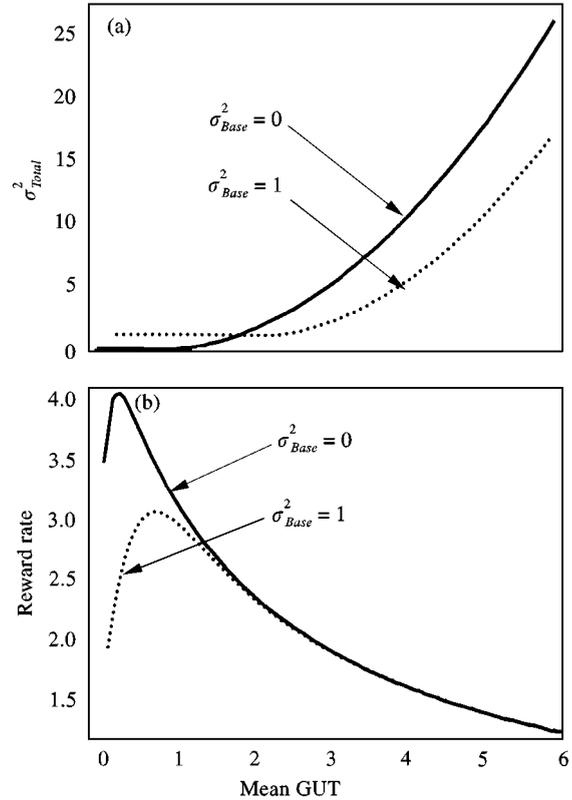

FIG. 3. (a) The total behavioral variances and (b) the expected reward rates to mean GUT given that base behavioral variance is each zero (solid line), and 1-unit (dotted line).

state, a single GUT should be adopted for each base variability. The base behavioral variability would reduce the long-term reward rate and increase the optimal GUT (Fig. 4).

Discussion

Many optimality models require the behavior of an animal under given conditions to be constant. However, observed behavior is nearly always variable. The variability of behavior should be considered a constraint in many ecological situations. The variability may be an unavoidable feature of behavior even in a completely constant or stationary environment. If the environmental state includes stochasticity, variability of behavior may often be much more unavoidable (Yoshimura & Shields, 1987, 1995). However, in some cases, variability is optimal and a mixed strategy is selected for (León, 1991; Levins, 1968; Sasaki, 1995).

Sit-and-wait predators often experience stochastic events in the patch exploitation process. The GUT adopted by sit-and-wait forager is often investigated in studies of foraging (Kamil et al., 1993; Nishimura, 1988, 1991, 1992). The variability of the GUT obviously decreases the reward rate below that of the optimal decision [see Figs. 3 and 4(b)]. However, in searching for the optimal decision, there exist two strategic options. When the forager searches for the optimal GUT starting with a long GUT, a mixed strategy is favored during the exploration process. The variance of the mixed strategy is sensitive to the constraint of base behavioral variability. The strategic variance is larger for small base behavioral variability. On the other hand, when the forager explores the optimum at short GUT, a single strategy is favored during the exploration process.

The unavoidable constraint, the base intrinsic variability of behavior, may be relaxed to some
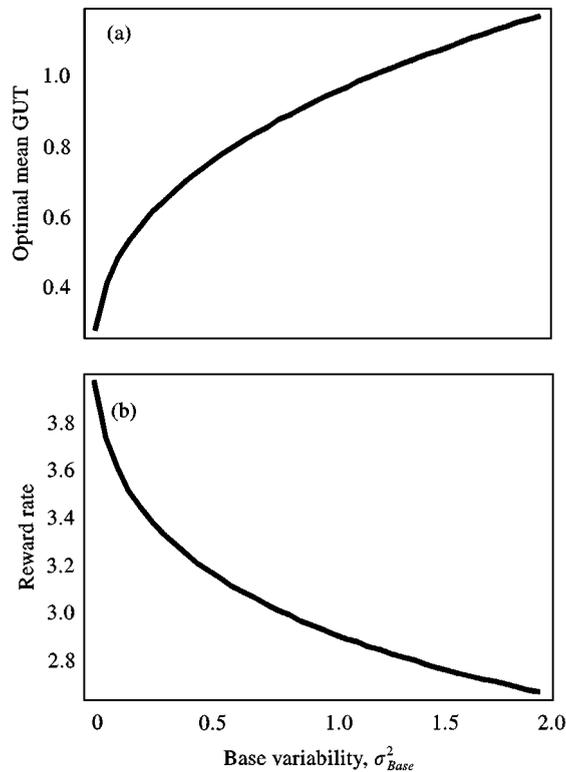
FIG. 4. Relationships between base behavioral variability and (a) mean GUT, and (b) reward rate in the optimal state.

extent with a reduction of ambiguity about the environment for the forager. In this paper, I did not explicitly address the learning and information acquisition process in an uncertain environment. During the search for the optimal GUT, the base behavioral variability would be reduced. If the forager explores the optimal GUT starting with a short GUT, it is imperative to reduce the base behavioral variability [see Fig. 3(b)]. On the other hand, if the forager explores the optimal GUT starting with a long GUT, the base variability is not a serious disadvantage at the beginning of exploration [see Fig. 3(b)].

Psychologists have found that behavioral variability is constrained in such a way that the mean and variance of performance are interrelated in a particular way; e.g. scalar timing in which the coefficient of variation is constant (Gibbon, 1977). Houston & McNamara (1985) analysed behavioral variability affecting foraging behavior according to the knowledge of the psychologists' studies. In this framework, a fixed relationship is assumed between mean and vari-

ance, e.g. $\sigma^2 = $ constant $\times \mu$, and the each statistic parameter is never affected separately by any external factor.

Psychologists' and behavioral ecologists' arguments have not been sufficiently combined with each other. Behavioral ecologists solve optimization problems with absorbed interest and psychologists concentrate on patterns and processes of behavior. I have also treated a source of behavioral variability as a constraint like several psychologists and behavioral ecologists have assumed (Gibbon, 1977; Gibbon et al., 1988; Houston & McNamara, 1985; Kacelnik et al., 1990; Kamil et al., 1993). I clarified that another source of behavioral variability is generated during the search for optimal decisions.

For a sit-and-wait forager, the prey-encounter rate is not high, and thus, the expected time to encounter prey is long. If it can be supposed that the forager searches for the optimal GUT starting with a long GUT, a mixed strategy should be adopted in the searching process. In the search for the optimal GUT, a strategic component would be involved in the variability of behavior.

Evolutionary ecologists tend to consider a sort of final optimal state. Behavioral ecologists also have a similar attitude to behavioral study. However, in natural conditions, it may be that several observed behaviors are in a transient state concerning optimal state. Thus, it is important to investigate transient states as well as stationary states in order to understand animal behavior.

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APPENDIX

The total behavioral variability is defined as $\rho(t|p(\mu), \sigma_{Base}^2) = g(t|\mu, \sigma_{Base}^2)\,p(\mu)$, where $g(t|\mu, \sigma_{Base}^2)$ is a gamma distribution and $p(\mu)$ is an arbitrary probability distribution with mean, $\tilde{\mu}$, and variance, $\sigma_{Strategy}^2$. Variance of t that follows with $\rho(t|p(\mu), \sigma_{Base}^2)$ can be derived by the definition of variance, $V[t] = E[t^2] - E[t]^2$, where the expectations are the weighted means with probability function, $\rho(t|p(\mu), \sigma_{Base}^2) = g(t|\mu, \sigma_{Base}^2)\,p(\mu)$:

$$V[t] = \int p(\mu)\left[\int t^2 g(t)\,\mathrm{d}t\right]\mathrm{d}\mu$$

$$-\left(\int p(\mu)\left[\int t g(t)\,\mathrm{d}t\right]\mathrm{d}\mu\right)^2$$

$$= \int p(\mu)\,(\sigma_{Base}^2 + \mu^2)\,\mathrm{d}\mu - \left(\int p(\mu)\,\mu\,\mathrm{d}\mu\right)^2$$

$$= \sigma_{Base}^2 + \sigma_{Strategy}^2 + \tilde{\mu}^2 - \tilde{\mu}^2 = \sigma_{Base}^2 + \sigma_{Strategy}^2.$$